University of Alberta

Arthropod biodiversity of *Populus* spp. coarse woody material in north-central Alberta

by

Harry Edward James Hammond ©

A thesis sunbmitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Department of Entomology

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Arthropod biodiversity of *Populus* spp. coarse woody material in North-Central Alberta** submitted by Harry Edward James Hammond in partial fulfillment of the requirements for the degree of Master of Science.

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Dedication

To my family,

Harry, Dena, Grant and Baby

Abstract

I studied arthropod diversity inhabiting *Populus* coarse woody material from aspen-mixedwood forests in north-central Alberta. More than 39,000 arthropods, primarily from the Acari, Collembola, Coleoptera, and Diptera, were collected between 1993 and 1995. Detailed analyses were restricted to the 257 saproxylic beetle species collected from rearings from wood and window-traps placed on snags. Beetle species richness and trophic structure was similar between collection methods; however, beetle abundance and the specific fauna collected differed between methods.

Spatial and temporal scale greatly influenced the distribution of saproxylic beetles across the landscape. Species richness and abundance was similar between regions, although there was a turnover in the particular fauna collected. Although standardized beetle abundance was higher in mature stands, faunal richness was higher in old-growth stands. Also, there was higher fungivore abundance in mature stands, and higher predator abundance in old stands, suggesting a change in the fauna during stand succession. Species diversity was similar in wood differing in decay, but a significant amount of niche partitioning occurred because there was a shift in species composition from minimally decayed to advanced decayed wood. Logs had slightly higher species diversity than snags, but snags tended to have a higher proportion of wood borers. Temporal variation also influenced catches of saproxylic beetles, suggesting that several years of collecting is required to adequately assess and monitor the fauna from dead wood.

Forest harvesting initially increased the diversity and abundance of saproxylic beetle assemblages. The beetle fauna collected from harvested old stands was more similar to old forest stands than to harvested mature stands, suggesting that faunal composition is not much affected for at least two years post-harvest. Implications of these findings for forest management are discussed.

Arthropods did not initially increase the rate of decomposition of new dead wood, but a unique fauna was associated with this resource. Three beetle species were abundant, and two more specialized, on new dead wood. Snags had a higher proportion of wood borers, and stumps and logs a higher proportion of predators, suggesting dispersal capabilities influence the fauna in dead wood.

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1. Background and Introduction

1.1 What is biodiversity?

The term 'biodiversity' was coined by Walter Rosen in 1986 for the National Forum on Biodiversity, and was defined as "the totality of hereditary variation in life forms, across all levels of biological organization, from genes to chromosomes within individual species, to the array of species themselves, to entire ecological communities" (paraphrased from Wilson, 1994 pg. 359; Wheeler, 1990), and has since been adopted by both the scientific community and the public. The concept of 'biological diversity' had been recognized for some time, with researchers in many disciplines defining and quantifying diversity differently. For example, geneticists focused on the hereditary aspects of biodiversity, *genetic diversity*, as the allelic or genotypic diversity within a population (Burton et al., 1992; Harris and Silva-Lopez, 1992); while others focused on how genetics and environment interact resulting in *phenotypic diversity*, referring to genotypic diversity and the morphological combinations resulting from the environmental context at which the genome occurs (Harris and Silva-Lopez, 1992). Ecologists extended these definitions further to describe diversity at different spatial scales, for instance *alpha diversity* refers to the number of species within a given community, site type, or ecosystem; *beta diversity* is the measure of the change of species spatially across larger areas, such as ecosystems; and *gamma diversity*, or landscape diversity, refers to species composition on similar site types across different regions (Boyle, 1992). The fundamental concept underlying these ecological definitions of biodiversity is that diversity is a function of the number of species and their abundance. This thesis focuses on these two constituents of the biodiversity concept in the context of development of species inventories for communities within the boreal mixedwood forest, and exploration of natural and man-made processes that determine community structure.

1.2 Current knowledge: a species inventory

Many estimates of the number of extant species have been ventured over the last two decades (Erwin, 1983; Wilson, 1988; 1992). Wilson (1985) admits that "...we do not know the true number of species on Earth, not even to the nearest order of magnitude"; but has estimated that the total number of species lies between 5-30 million (Wilson, 1988). Erwin (1983) estimated, based on his collections of insects from the canopies of trees in tropical rain forests, that there are over 30 million species of insects alone. If Erwin's estimate of 30 million insect species is correct, of which only 750,000 have been described (Wilson, 1988), that means approximately 97.5% of all insect species are undescribed. Most undescribed species are microorganisms (viruses, bacteria, and protozoans), the invertebrates, and lower plants (including the fungi). Furthermore, we really know very little about the biology of the vast majority of the species that have been described. At the current level of resources devoted to taxonomy and systematics, it will require hundreds of years to even fully describe the global biota, let alone explore the biology of each species. Sadly, if current trends continue, most of this biodiversity will be lost before it has been described.

1.2.1 The biodiversity crisis

Loss of biodiversity has become a global concern (Wilson, 1988, 1992, 1994; Wheeler, 1990; Burton et al., 1992). Species are the basic building blocks of food webs, communities and ecosystems. Species are important to the ecosystem in many ways. A few important examples include: as integral components of nutrient cycles (Krebs, 1978), as measures of environmental quality and detoxification of polluted systems (Bishop and Cook, 1981), and key players in decomposition processes (Crossley, 1976; Holldobler and Wilson, 1990). In addition, species have their own intrinsic value. The many taxa that comprise the biological communities within ecosystems are the 'nuts and bolts' responsible for its function, health and resilience following disturbance. Excessive loss of species will alter properties of ecosystems and compromise their ability to rebound following disturbance. Given our poor knowledge of the ecological roles of most species, extreme caution is recommended to prevent thoughtless loss of potentially important components of ecosystems.

From a human perspective, species are important as long term food resources and as sources of pharmaceuticals. Approximately 90% of food consumed by humans comes from 15 main plant species and eight animal species (Pimental et al., 1992), even though several thousand other plant species are consumed by humans, and hundreds of other animal species are available as food reserves. Many species are crucial to medicine, mainly by their use in developing new and superior pharmaceutical agents (Wilson, 1992). Over 40% of pharmaceuticals in use in the United States are derived from other species, of which 25% are extracted from plants, 13% percent from microorganisms and 3% from animals (Wilson, 1992). Hundreds of prescription drugs have been formulated from newly discovered tropical plants and by the advice given by aboriginals who have used their healing powers for thousands of years (Wilson, 1992).

The reduction in species number is chiefly due to escalation of human numbers, movement of humans into previously unsettled areas, and industrialization that has destroyed previously pristine habitats (Wilson, 1992; Pimental et al, 1982). As the human population grows, increased stress is placed on the environment because each new person competes with the earth's biota for space and resources (Pimental, 1992); thus, driving species loss and extinction. Humans are constantly exploring new areas which results in the exploitation of previously unused resources, habitat destruction, pollution and the introduction of species into non-native areas, sometimes resulting in competitive exclusion of native species. The key to preserving biodiversity requires (from Wilson, 1988, 1992; Pimental et al., 1992):

1) development of measurement and monitoring tools for assessing the role organisms play in the environment.
2) development and encouragement of ecologically sound management practices in resource-based industries to protect habitat and promote sustainable development.
3) encouragement of family planning in an attempt to control human population growth.
4) education of society to value biological diversity and to express their concerns to scientists, farmers, foresters, industrialists, policy makers and concerned people.

1.3 Biodiversity research in the boreal forest of Alberta

The northern boreal forest in Canada extends from the Maritimes in the east, south through Quebec and Ontario, and north-west through the prairies up into northern Yukon. This region contains a mosaic of different forest types, from the vast northern subarctic coniferous forests including such species as white spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) B.S.P.), tamarack (*Larix laricina* (Du Roi) K. Koch) and balsam fir (*Abies balsamea* (Linn.) Mill.)., to the more southern aspen grove, or more commonly aspen-mixedwood or boreal mixedwood ecotone (Figure 1-1), with such characteristic species as trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.) and paper birch (*Betula* spp.) (Scudder, 1979). Hunting, trapping and fishing by many aboriginal groups have been the traditional land uses of this area (Stelfox, 1995).

The province of Alberta, in the last several decades, has seen a dramatic increase in use of aspen and poplar as economically valued tree species. Much of Alberta's aspen-mixedwood forests have been allocated for harvest of aspen, poplar and white spruce for pulp, paper, and oriented strand board (Figure 1-2) (Stelfox, 1995). In 1971, harvesting of aspen and poplar represented only 2% of the annual cut, but over the last 23 years has dramatically increased to 73% in 1994 (Peterson and Peterson, 1992; Alberta Land and Forest Service, 1994). The forest industry in Alberta generates approximately $456 million in wages, $846 million from export and lumber, and employs over 29,000 people (Anonymous, 1993). Because this forest type in Alberta, and subsequently Canada, has never been previously exploited, there are no projections on the effects of large scale aspen-based forestry on ecosystem health.

Proposed development of the aspen-mixedwood forest in Alberta has evoked concern over the effects of large scale disturbance upon the flora and fauna of this region. A multi-disciplinary study was set up in 1992 to research the structure and biodiversity of habitats found in aspen-mixedwood forests. The study included work on climate, coarse woody material dynamics, understory floral species composition and dynamics, and bird and mammal composition within these forests (Stelfox, 1995). Arthropods, including the epigaeic and phytophagous insect communities were also studied (Spence and Langor, 1994; Spence et al, 1997). One community that was targeted as potentially sensitive to disturbance was the arthropods that decompose coarse woody material.

1.4 Coarse woody material and biodiversity

1.4.1 Definitions and roles of coarse woody material

Coarse woody material (CWM) is the term given to the various forms of clearly discernible rotting wood found in forested and stream ecosystems (Harmon et al., 1986). Coarse woody material includes snags, which are standing dead trees, stumps, which are the basal portion of snags (or snags less than about 2 m tall), and logs, which are fallen snags, as well as the large branches and coarse root systems of trees (Harmon et al., 1986). Factors that create CWM include: 1) wind, which uproots or snaps trees and breaks branches, or kills single trees or clusters of trees; 2) fire, which directly girdles stems, scorches crowns, and burns root systems; 3) insect pests, which girdle stems, repeatedly defoliate trees which causes stress and predisposes the tree to attack by other insects or disease, and introduces pathogens; 4) diseases, which interrupt water and nutrient movement through the tree, or cause premature decay; and 5) suppression and competition; mortality due to slow growth by competition by other trees (Harmon et al., 1986).

Many ecological roles are served by CWM in the forest ecosystem, and understanding of these roles is crucial to forest management. First, CWM affects geomorphology, through effects on topography and land forms, and on transport and storage of soil and sediment (Harmon et al., 1986). Root throw of uprooted trees results in substantial soil mixing and heterogeneity, whereas logs and stumps with their associated root systems can control downslope movement of water and litter, and can act to hold soil together preventing soil erosion.

A second major role of CWM is its influence on terrestrial nutrient cycles and carbon budgets. Snags and logs account for up to 45% of all above ground organic matter storage; and are responsible for up to 21% of above ground nitrogen, phosphorus and calcium storage (Harmon et al., 1986). Foliage is recognized as the primary organic matter input in aspen-mixedwood systems, but tree death is responsible for 24-39% of total organic matter returned to forest floors (Peterson and Peterson, 1992). Wood is qualitatively different from other organic inputs to the soil, and thus plays important ecological roles independent of its function in organic matter build up and nutrient cycling. Once wood has died, insects, fungi, and bacteria act to break the wood down and return the nutrients to the soil.

Third, CWM provides habitat for other organisms (Harmon et al., 1986). Many autotrophic taxa are associated with CWM and include: green algae, diatoms, blue-green algae, fungi, lichens, liverworts, mosses, clubmosses, horsetails, ferns, gymnosperms and angiosperms. There are many ways in which plants can use CWM: some plants simply spread their roots along the surface of the wood, and are thus considered epiphytes; others have roots that easily invade rotting wood and can extract large amounts of water and nutrients; others root on the fine mat of litter that can accumulate on the top of logs and stumps; and some shade-tolerant species, such as white spruce, are dependent on CWM for regeneration. Plants growing on CWM add organic matter as they die, or trap fine litter that would most likely be lost from the wood surface (Harmon et al., 1986).

Coarse woody material is well documented as habitat for small and large vertebrate species (Cunningham et al., 1980; Brady, 1983; Winternitz and Cahn, 1983; Reynolds et al., 1985; Ralph et al., 1991). Rotten trees provide holes and cavities for many nesting birds to build nests and raise young. These same cavities are also available as nesting sites for bat species (Stelfox, 1995). Many amphibians, reptiles and small mammals nest in moist logs, or simply use them as hunting grounds to find their prey (Stelfox, 1995).

In addition to the other plant and vertebrate species, many invertebrate species are also associated with coarse woody material. These invertebrate species are responsible for wood decomposition, either directly, in the case of wood feeders, or indirectly, as vectors of pathogenic fungi (Reichle, 1977). Interactions between the multitude of bacteria, fungi and arthropods profoundly affect the initiation and rate of wood decay (Reichle, 1977).

1.4.2 Saproxylic invertebrates and the loss of biodiversity

A saproxylic invertebrate is one that is dependent during some part of its lifecycle upon: 1) wood, phloem or bark of moribund or dead trees (standing or fallen) for shelter or food; 2) wood-inhabiting fungi for food; or 3) the presence of other saproxylics in mutualistic, symbiotic, predatory or parasitic relationships (Speight, 1989). Saproxylic species are profoundly affected by habitat fragmentation due to forest harvesting, agriculture, oil/gas exploration and other human activities (Heliövaara and Väisänen, 1984; Speight, 1989; Mikkola, 1991; Warren and Key, 1991). In Europe, centuries of forest harvesting and subsequent replanting of native and non-native conifer tree species have been implicated in an 80% drop in faunal diversity, especially among the saproxylic community (Speight, 1989).

Previous studies of saproxylic communities have focused on those associated with conifer species (Graham, 1925; Savely, 1939; Wallace, 1953), presumably due to their economic value. Aspen and poplar are increasingly important economic tree species in Alberta. The high percentage of biomass composed of non-marketable wood in mature aspen-mixedwood forests (Peterson and Peterson, 1992) suggests that we should know more about the saproxylic biota in order to evaluate the importance of CWM in mixedwood forests. Arthropods are an appropriate model for study because: 1) they are taxonomically and ecologically diverse, and include species that are endemic to localized areas and microhabitats, 2) most have large population sizes, 3) they are easy to sample using simple and inexpensive methods, and 4) they can be stored indefinitely and inexpensively for future study (Kremen et al., 1993). Arthropods are also sensitive to environmental variation, and are thus potentially good 'indicator' species for assessing the effects of habitat perturbations (Kremen et al., 1993).

Saproxylic arthropods are essential elements of forest ecosystems. Their roles in nutrient cycling and decomposition may influence long-term forest productivity and sustainability. Thus it is also important to determine how forestry activity affects the diversity of saproxylic species in forest communities.

1.5 Overall objectives of thesis

The general objectives of this study are :

1) To describe the saproxylic arthropod community found in CWM originating from *Populus tremuloides* Michx. and *P. balsamifera* L. in the boreal mixedwood forests in central and northern Alberta, and to review and critique the various methods of collecting this fauna.

2) To describe variation in the Coleoptera fauna associated with CWM at several spatial scales: between regions (Lac la Biche and Eureka River), between different age classes of forest stands, between varying decay levels of the wood, and between logs and snags, and to describe how beetle dynamics changes temporally.

3) To describe the immediate effects of clear cut harvest on the saproxylic beetle community.

4) To describe the early colonization of newly-created CWM by insects and their role in initiating and regulating decomposition of new dead wood.

Chapter Two focuses on the arthropod fauna as collected using two methods: rearings of insects from removal of snags and logs from forests, and sampling on snags within forests with modified window-traps. I examine the biases of different collecting methods, and provide a detailed study of the Coleoptera assemblage within rotting wood. Also, I present a brief discussion of the biology of the Coleoptera groups collected, their possible roles within the forest, and new provincial records.

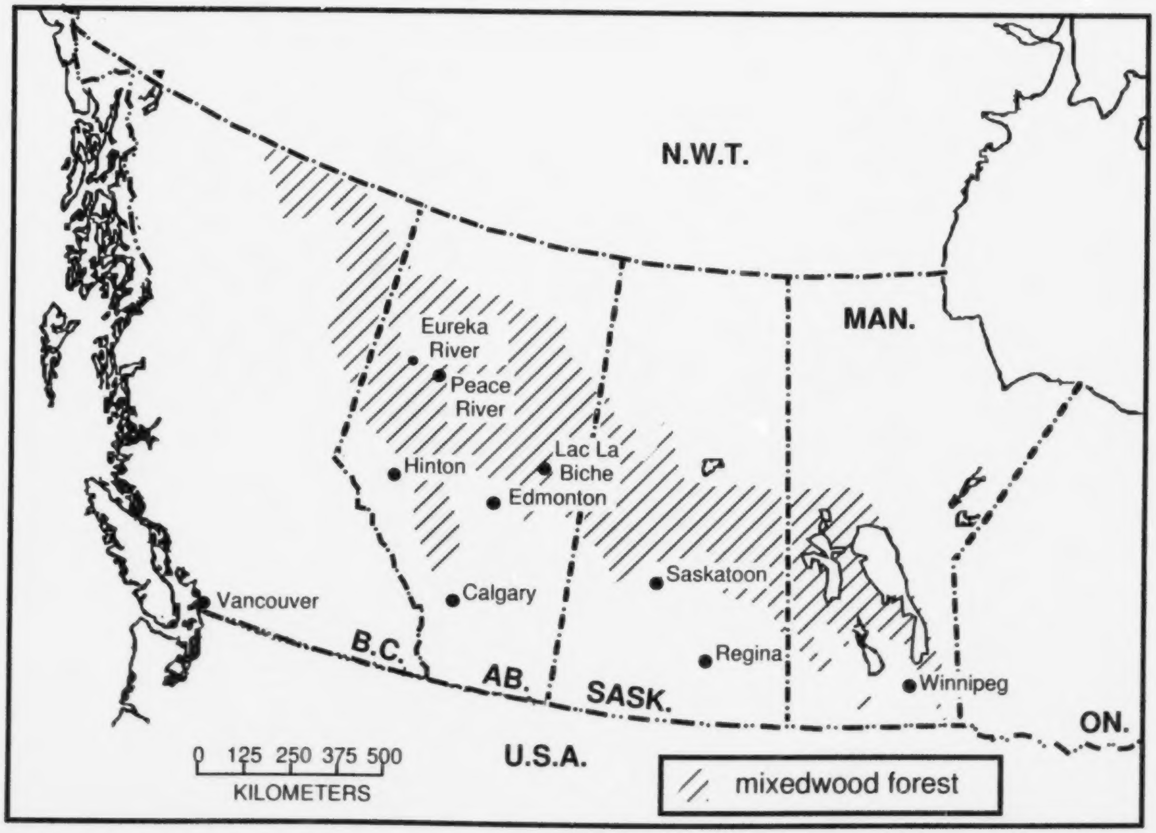
I examine variation in the Coleoptera fauna across different spatial scales and temporal scale in Chapter Three. I use several different diversity measures with rearing and window-trap data to answer the questions: what is the influence of region, age structure and decay class on the beetle fauna found in snags?

Chapter Four focuses on the immediate effects of clearcutting on the saproxylic beetle fauna. I compare beetle abundance and diversity from forest stands and two-year-old clear cuts at Lac la Biche in 1995. This data is the first to directly measure the effects of clear cut harvest on saproxylic faunas.

In Chapter Five, I discuss an experiment which measured the colonization of newly created CWM by arthropods, and the impact they have on initial decomposition of wood. I compared wood hardness (*i.e.* a measure of wood decay) between unscreened wood, which was exposed to insect attack, and screened wood, which was covered with insect mesh to prevent infestation of the wood by insects. I also propose a mechanism for insect colonization and decomposition of *Populus* wood.

I summarize and discuss my results with respect to determinants of structure and spatial distribution of the saproxylic community in Chapter

Six. I will present recommendations to aid forest managers in developing harvest plans that are sensitive to emerging concerns about biodiversity.


N.W.T.
MAN.
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0 125 250 375 500
KILOMETERS
mixedwood forest

Figure 1-1. Distribution of the aspen-mixedwood forest type in the prairie provinces of Canada. Arthropods in this study were collected from Eureka River (56° 51' N, 118° 37' W) and Lac la Biche (54° 51' N, 111° 27' W).

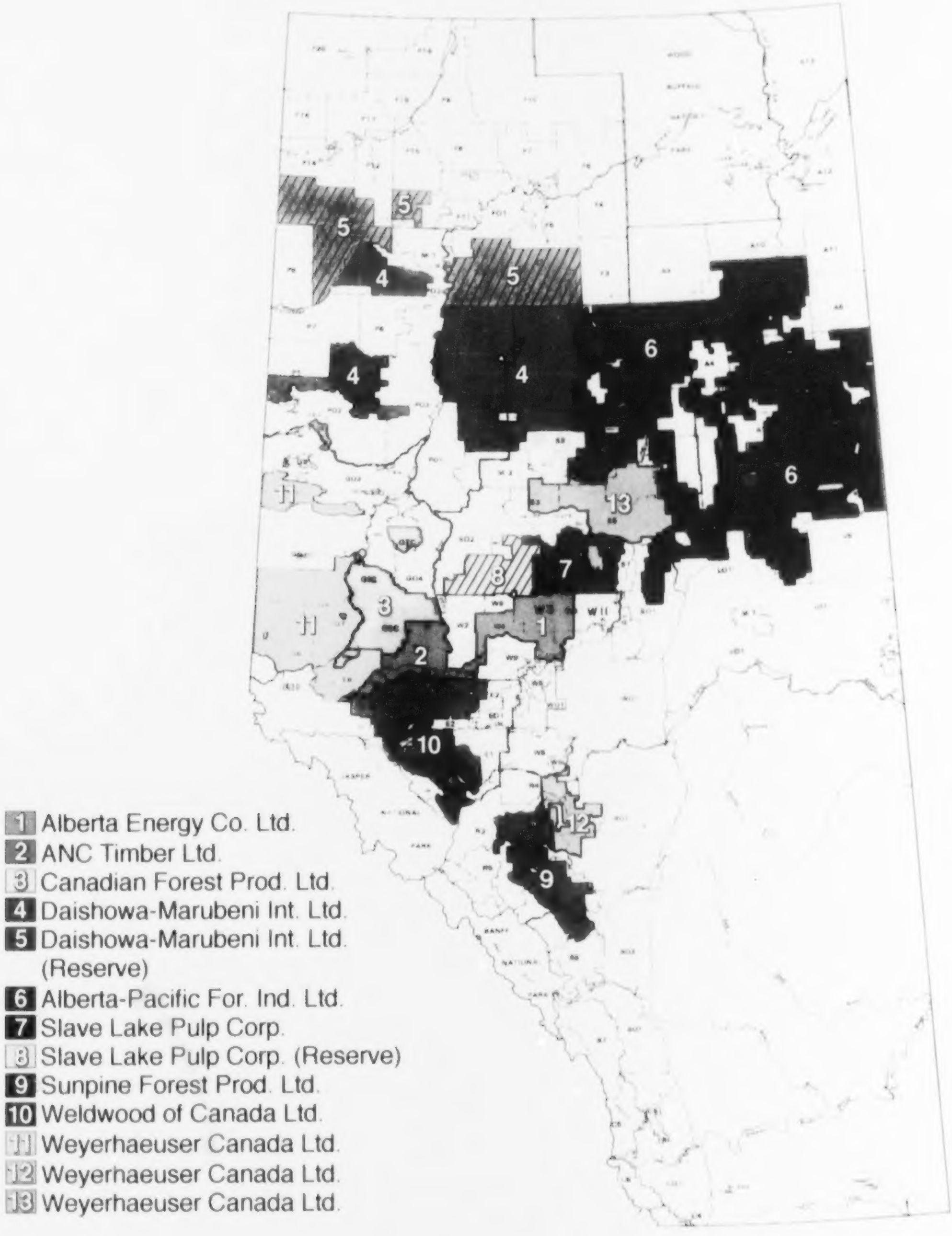
1 Alberta Energy Co. Ltd.
2 ANC Timber Ltd.
3 Canadian Forest Prod. Ltd.
4 Daishowa-Marubeni Int. Ltd.
5 Daishowa-Marubeni Int. Ltd. (Reserve)
6 Alberta-Pacific For. Ind. Ltd.
7 Slave Lake Pulp Corp.
8 Slave Lake Pulp Corp. (Reserve)
9 Sunpine Forest Prod. Ltd.
10 Weldwood of Canada Ltd.
11 Weyerhaeuser Canada Ltd.
12 Weyerhaeuser Canada Ltd.
13 Weyerhaeuser Canada Ltd.

Figure 1-2. Forest management agreements in Alberta as of January, 1995.

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2. Collection and Inventory of Arthropods from *Populus* Coarse Woody Material, with Emphasis on the Coleoptera

2.1 Synopsis

Arthropods associated with *Populus* coarse woody material (CWM), were sampled from aspen mixedwood stands in north-central Alberta using rearings from wood bolts and modified window-traps attached to snags. More than 39,000 arthropod specimens were collected over three years, comprised mainly of Coleoptera, Diptera, Hymenoptera and Acari. Detailed analyses comparing the number of species, standardized abundance, and trophic structure from each collecting method were restricted to the 257 saproxylic species of Coleoptera. Abundance of beetle species, from both rearings and window-traps, approximated lognormal distributions. Rarefaction estimates of species richness from rearings and window-traps indicate little difference in the expected number of species collected by each method. However, the abundance of particular beetle families differed significantly between methods. Fungivorous and predatory beetles were more abundant in CWM than wood borers, scavengers, or taxa with undetermined habits, with beetle trophic structure similar between collection methods. A combination of collecting methods is recommended for arthropod inventories from CWM.

2.2 Background and objectives

A large and diverse arthropod fauna uses snags, stumps, logs, and other forms of coarse woody material (CWM) for food, shelter, foraging or reproduction. Many of these species are saproxylic and thereby depend, during some part of the lifecycle, upon dead wood, wood inhabiting fungi, or the presence of other saproxylics (Speight, 1989). Saproxylic organisms are important components of forest ecosystems, and play vital roles in decomposition and nutrient cycling. In North America saproxylic arthropods have been little studied, only from economically important tree species such as larch, pine and oak (Blackman and Stage, 1918; Savely, 1939; Howden and Vogt, 1951). However, saproxylic arthropods are much better known in Europe (Palm, 1951, 1959; Wallace, 1953; Fager, 1968; Speight, 1989; Väisänen et al., 1993; Siitonen, 1994; Siitonen and Martikainen, 1994), where centuries of forest harvest and subsequent reforestation with native and non-native conifers has been implicated in a significant drop in diversity of saproxylic insects (Heliövaara and Väisänen, 1984; Speight, 1989; Siitonen and Martikainen, 1994). In Canada, there have been a few studies of guild structure of saproxylic insect assemblages (e.g. Pielou and Verma, 1968), but most work has focused on the taxonomy and biology of a few pest taxa (e.g. Barter, 1965; Bright, 1976, 1987). Little is known about the response of saproxylic faunas to forest management.

Harvesting is quickly replacing wildfire as the major disturbance in boreal mixedwood forests in central and western Canada as aspen has become an economically valued timber species. For example, harvest of aspen in Alberta has been steadily increasing, from 2.4% of total volume cut in 1980-81 to 73% in 1994, and is still growing (Peterson and Peterson, 1993, Alberta Land and Forest Services, 1994). Expansive development of these forests gives rise to concerns about sustainability and long term maintenance of ecosystem integrity. In particular, much attention has focused on implications for biodiversity (Stelfox, 1995; Spence et al., 1996, 1997) as an indicator of healthy forest systems.

To predict the effects of disturbance on a community, we must first assess community composition and structure, and determine how this varies spatially and temporally before disturbance. However, the physical characteristics of CWM (size, weight, and durability due to decay) make it difficult to sample arthropods quantitatively. In addition, several microhabitats such as non-vascular plants and fungal fruiting bodies, offer a diversity of places for insects to feed and oviposit, often making sampling difficult. Early published accounts of faunistic studies of dead wood used several simple methods for determining the insect fauna, including 1) inspection of insect emergence holes and damage (Graham, 1925), 2) observations of insects moving to and from dead wood (Howden and Vogt, 1951), 3) hand collecting (Blackman, 1924; Savely, 1939, Wallace, 1953; Fager, 1968), and 4) a combination of hand collecting and rearings (Blackman and Stage, 1918; Savely, 1939, Wallace, 1953; Fager, 1968). Recently however, there has been a concerted effort to evaluate and design better methods to quantitatively sample this fauna, such as various flight intercept traps (Käila, 1993; Käila et al., 1994; Jonsell and

Nordlander, 1995) and hand collecting methodologies (Väisänen et al., 1993; Siitonen, 1994; Siitonen and Martikainen, 1994).

In this chapter I compare the utility of rearings and window-traps for collection of arthropods from *Populus* CWM, and present an inventory of arthropods collected from northern Alberta using these methods. The relative abundance of each arthropod group was compared between methods. The Coleoptera were used for more detailed comparisons of methods with respect to number of species, mean standardized abundance, species-abundance relationships, and trophic structure, because 1) this order is relatively well known in Canada with regard to taxonomy and distribution (e.g., Bousquet, 1991), 2) is taxonomically and trophically diverse, and represents a large proportion of the groups found in dead wood (Speight, 1989), 3) is easy to preserve and store for later identification, and 4) allows comparisons to other studies of CWM which focused on beetles.

2.3 Materials and methods

2.3.1 Study sites.

Arthropods associated with *Populus* CWM were sampled from boreal mixedwood stands near Touchwood Lake, east of Lac la Biche (54° 51' N, 111° 27' W), and near Eureka River (56° 35' N, 118° 37' W) north of Fairview, Alberta. The four forested stands at each location were primarily dominated (>80% of canopy and understory trees) by trembling aspen (*Populus tremuloides* Michaux), but also included balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss), and birch (*Betula* spp.). These stands ranged in age from 40 to >100 years since last disturbance by wildfire. In each stand, the standing snags and fallen logs sampled ranged in size from 9-48 cm diameter at breast height (DBH) and represented the various degrees of stem decay found in these stands.

2.3.2 Collection methods and identification

Snags and logs of *Populus tremuloides* and *P. balsamifera* are often difficult to distinguish, especially those of large diameter and advanced decay. Therefore, insect data was not partitioned by tree species.

Arthropod rearings. In late April and early May of 1993 and 1994, bolts 1.2 m in length were cut from the base, center and top of each

Populus snag and log sampled. Three snags and three logs, representing various degrees of stem decay, were sampled in each of two stands in each region. Bolts were sealed in plastic bags and transported to the Northern Forestry Center in Edmonton. The ends of each bolt were sealed with paraffin to slow moisture loss, and the three bolts from each snag or log were placed together in a rearing cage and held at ambient temperature and light.

Each rearing cage (Figure 2-1) consisted of three wooden walls and a front door, each 1.5 m in width and 1.5 m in height. The floor consisted of strong welded wire mesh. The roof originally was a square pyramid constructed of thin polyethylene plastic, with a funnel and bottle hanging from the apex, to collect insects that flew upward; however, few insects were so collected in the first year, and the pyramid was replaced in 1994 with sheets of plywood to form a flat roof. Under the floor an inverted square pyramid, constructed of thin polyethylene plastic, with a jar at its apex, collected most specimens. The collecting jars contained ethylene glycol as a killing agent and preservative.

Wood samples remained in rearing cages for one year and then were subsequently replaced with fresh samples. Arthropods emerging from CWM samples were collected weekly (biweekly in September) and sorted in the lab. To sort microarthropods, each sample was poured through fine filter paper lining a Buchner funnel, which was sealed to the top of a side port Erlenmeyer flask. A vacuum line connected to the side port of the flask enabled each sample to be filtered under pressure. Microarthropods remaining on the filter paper were subsequently preserved in 95% ethanol.

After termination of rearing, the volume of each bolt was estimated by measuring its diameter at the center of its length and calculating the volume of a cylinder 1.2 m in length. The volumes of the three wood bolts in each cage were then summed to give a total for each snag and log sampled.

Window-traps. Window-traps, modified from Käila (1993), were used to sample insects flying to and from snags (Figure 2-2). Traps consisted of a sheet of clear plastic, 1.5 mm x 20 cm x 30 cm, fastened perpendicularly to the trunk with two pieces of wire. A pack-cloth funnel was fastened to the lower edge of each window with wire. The lower end of the funnel consisted of a circular piece of plastic cut from 'sump pump' hose, attached to the funnel internally with silicon, and externally with two pieces of wire, to form a 'lip'. A whirl-pak™ bag was then fastened over the lip using a hose clamp. The bag was partially filled with ethylene glycol as a killing agent and preservative. Each bag was then shielded with a welded wire tube to prevent damage by small mammals.

Two window-traps, one with the top of the window at breast height (ca. 1.3 m) and the second with the top of the window at ca. 2.0 m were placed on each snag. Both traps on each snag were oriented in the same cardinal direction, as determined randomly by dice roll. Nine snags, representing the various degrees of stem decay, were sampled in four forested stands at each region in 1994 and 1995. The same snags were subsequently sampled in both 1994 and 1995, if possible. If snags fell down, a new snag was picked that was similar in size and position in the stand to the fallen snag. Insects were collected biweekly 18 May-7 October, 1994 and 2 May-28 August, 1995.

Beetles collected by each method were identified to species or species group. The other arthropods were identified to the lowest taxonomic level possible based on available literature and local taxonomic expertise. All arthropods collected are stored in a large synoptic collection at the University of Alberta.

2.3.3 Data analyses

The proportion of each arthropod group collected by each trapping method is presented to facilitate visual comparisons of the catch across trapping methods, and with data from other studies of arthropods from CWM.

Detailed analyses were restricted to saproxylic beetles (Speight, 1989). To account for differences in sampling effort (time and wood volume), saproxylic beetle abundance was standardized to 1000 trapping days and 0.1 m^3 of wood for rearing data, and to 1000 trapping days for window-trap data.

Beetle species-abundance relationships were constructed using Whittaker plots of total abundance (y axis) and rank order of species (x axis) (Krebs, 1989). Whittaker plots are a visualization technique useful to determine whether the frequency distribution of species conforms to a logseries (linear relationship between species abundance and its rank), or a lognormal distribution (reverse S shaped curve). The data were fit to the appropriate model, and the fit tested using a Chi-Square test.

The number of species represented by each beetle family collected was compared among trapping methods using Chi-Square. Beetle families where the expected number of species was less than one were not included in analysis (Everitt, 1977). Mean standardized abundance of each beetle family was compared among methods using a paired t-test. To correct for uneven catches when comparing species richness, I used rarefaction, a method of estimating the number of species expected in a random subsample drawn from the larger sample (Hurlbert, 1971). The resulting value can be interpreted as a 'diversity index' because the method takes into account both species richness and abundance. In addition, cluster analysis of Bray-Curtis percent similarity calculations, with group averaging as the weighting procedure (software by Ludwig and Reynolds, 1988) was used to compare assemblages between sampling methods.

To compare beetle trophic structure between collecting methods, each species was assigned one of the following four trophic roles according to information from the literature and advice from expert coleopterists: 1) predators, feeding mainly on other living arthropods; 2) fungivores, feeding mainly on fungi; 3) wood borers, any xylophagous, phloeophagous or wood boring beetle; and 4) scavengers, any detritivore, saprophore, or has several feeding habits. If the feeding habits of a species was uncertain, it was placed in the 'unknown' category. The distribution of the number of species representing each trophic role was compared between methods using Chi-Square. The mean standardized abundance of each trophic role was compared between methods using a paired t-test.

2.4 Results

A total of 39,094 arthropods, representing 5 classes, 13 orders, at least 113 families, and over 2000 species were collected from CWM in boreal-mixedwood forests over the three years of this study (Tables 2-1 and 2-2). Of these, at least 1500 species are estimated to be saproxylic.

The Acari were the most abundant group collected from rearings (Figure 2-3A), but not surprisingly was one of the least abundant groups in window-traps (Figure 2-3B). Other flightless groups (excluding Araneae) also had a greatly reduced abundance in window-traps as compared to rearings. Taxa colonizing CWM by flight, such as Diptera, Coleoptera, and Hymenoptera were relatively abundant in rearings, but dominated numerically in window-traps. These orders were generally characterized by large yearly fluctuations in relative abundance (Figure 2-3).

A total of 10,833 beetles were collected representing at least 372 species (Table 2-2). Fifty species of beetles, 90% of which were saproxylic, (Table 2-2) are new provincial records (Bousquet, 1991). Of the 257 saproxylic beetle species collected, 161 species, representing 1741 individuals, were collected in rearings; while 204 species, representing 7829 individuals, were collected in window-traps. A total of 108 species were collected by both methods.

Inspection of Whittaker plots was inconclusive as to which model better fit the observed saproxylic beetle species-abundance data (Figure 2-4), therefore the data were compared statistically to both logseries and lognormal models. Data from rearings were significantly different from expected values of a logseries distribution (χ^2=539.12, df=155, P<0.001) but were adequately modeled by the lognormal distribution (χ^2=8.24, df=10, P=0.61). The fauna collected by window-traps also fit a lognormal distribution better than a logseries (logseries: χ^2=2021.73, df=194, P<0.001; lognormal: χ^2=11.31, df=11, P=0.66).

The distribution of the number of species in each family did not depend on collecting method (χ^2=14.15, df=33, P=0.9983) (Table 2-3), but the mean standardized abundance of each family collected differed significantly among methods (t=2.97, df=50; P=0.0045) (Table 2-3). A comparison of saproxylic beetle species richness among trapping methods, using pooled data collected between 1993-95, showed that rearings tended to have higher species richness compared to window-traps (Figure 2-5A). However, rarefaction estimates of species richness from 1994, the only year in which both methods were used, were similar between methods (Figure 2-5B).

In general, fungivorous and predatory beetles dominated rearing and window-trap catches (Figure 2-6). The distribution of the number of species of each trophic role was similar between methods (χ^2=1.12, df=4, P=0.8897), as was the mean standardized abundance (t=2.20, df=4, P=0.0923) (Table 2-4).

2.5 Discussion

2.5.1 Arthropod inventory

The arthropod fauna associated with *Populus* coarse woody material is large and diverse. Although not all taxa were identified to species level, I estimate that over 1500 species of saproxylic arthropods were collected over the course of this study (Tables 2-1 and 2-2). A large proportion of this fauna is comprised of taxa that are species-rich but poorly known, such as the Acari, Collembola, Diptera and Hymenoptera (Figure 2-3). Danks (1979), in his review of the Canadian insect fauna, has estimated that approximately 50% of insects and 70% of arachnids remain to be described in Canada. Application of these percentages to the faunal lists generated by this study suggests that approximately 600-800 of the collected saproxylic species are undescribed. Given the importance of these faunas to forestry and agriculture, due to their influence on soil structure, decomposition processes and nutrient cycling, much more work is required to census and describe these groups.

There have been several inventories of arthropods associated with CWM. Savely (1939) listed 100 insect species and another 24 invertebrate species collected from short leaf and loblolly pine. He also listed 156 invertebrates including 122 insect species collected from oak logs. The Coleoptera, Diptera and Hymenoptera were the dominant groups in both lists. A total of 184 species of arthropods were collected from pine snags in Maryland (Howden and Vogt, 1951) and over 120 insect species recorded from pine stumps in England (Wallace, 1953), with the Coleoptera dominating the fauna. The invertebrate fauna colonizing natural and 'artificial' oak logs in England included 182 arthropod species, primarily comprised of the Acari, Collembola and Diptera (Fager, 1968).

Similar to previous studies of other trees, the fauna associated with *Populus* CWM was numerically dominated by Acari, Coleoptera, Diptera and Hymenoptera (Figure 2-3). These taxa typically dominate faunas associated with habitats that include large amounts of decaying organic matter, such as found in CWM, litter and soils (Pielou and Verma, 1968; Wagner et al., 1977; Harmon et al., 1986; Speight, 1989; Chandler, 1991; Väisänen et al., 1993; Battigelli et al., 1994; Käila et al., 1994; Siitonen and Martikainen 1994; Spence and Langor, 1994; Jonsell and Nordlander, 1995). It is generally accepted that the early ancestors of many insect groups (Entognatha, Apterygota), and especially beetles, lived under bark, and that their feeding habits and body forms, to some extent, have co-evolved (Evans, 1975; Daly et al., 1978; Crowson, 1981; Ponomarenko, 1995). Many of these taxa are saprophages, fungivores and entomophages, and thus occupy trophic roles which are well suited to life under bark.

2.5.2 Beetle diversity in coarse woody material

Coleopterans were among the most abundant taxa collected from *Populus* CWM. A total of 372 species were collected during this study, of which 257 are thought to be saproxylic (Table 2-3). In addition, approximately 40 of the 'non-saproxylic' beetle species collected are thought to overwinter in *Populus* CWM, and, hence depend on CWM to some extent. Coleoptera families with the highest species richness include the Staphylinidae (approximately 80 species), Carabidae (27 species), Leiodidae (12 species) and the Elateridae and Lathridiidae (approximately 10 species each)(Table 2-2).

The beetle fauna from *Populus* CWM in Alberta is more diverse than that known from CWM of other tree species. In a study of dead birch and birch decaying fungi in Finland, Käila (1993) reported 234 beetle species, with species richness highest in the Staphylinidae, Leiodidae, and the Ciidae (=Cisidae). In another study, Käila et al. (1994) compared the saproxylic fauna from dead birch and birch fungi between Finland and Russian-Karelia. They reported 158 species, among which, highest species richness, was recorded from the Elateridae, Leiodidae, Ciidae, Melandryidae and Cerambycidae. The beetle fauna from Scots pine and Norway spruce CWM from primeval and managed forests in central Finland included 107 species (Väisänen et al., 1993) but, unfortunately no information was presented about species richness of the families represented. Caution, however, must be exercised in comparisons among these studies because faunal differences cannot be clearly attributed to tree species. Comparisons are also confounded by geography, spatial scale, and management history of these forests.

The saproxylic beetle fauna from Alberta, however, is less rich than that recorded from Sweden. Palm (1959) recorded 342 saproxylic beetle species from *Populus tremula* L. in middle and southern Sweden. Of these, 12 were restricted to *P. tremula*, and 17 species overwintered. The distribution of species among families is significantly different between Sweden and Alberta (χ^2=82.36, df=39, P<0.01) (Table 2-5), as is trophic structure (χ^2=28.42, df=4, P<0.01) (Table 2-6). Predators and fungivores dominated CWM faunas in Sweden and Alberta, however, predators were dominant in Alberta whereas fungivores dominated the Swedish fauna (Table 2-6). Although both studies sampled roughly the same latitudes (54° to 59° N) and amount of area, Palm (1959) sampled 16 sites compared to two sites in Alberta. Thus, more extensive sampling in Sweden may partially explain the larger fauna collected because there is a positive relationship between sampling intensity and number of taxa collected (e.g., May, 1975; Krebs, 1989). Also, Sweden's fauna is taxonomically better known than Alberta's. Thus, the number of Alberta species may be underrepresented. For example, Aleocharinae collected in Alberta were not all identified to species, whereas 49 species were recorded from Sweden. If these are eliminated, the faunas are more similar in richness with 252 recorded from Alberta and 293 from Sweden. Differences in evolutionary history, glaciation patterns, climate, and forest management between Alberta and Sweden also influences faunal composition.

Palm (1951) also recorded 231 saproxylic beetle species from *P. tremula* sampled in northern Sweden. This is not as species-rich as the more southern fauna (Palm, 1959), and demonstrates the pattern of decreasing species richness with increasing latitude (Fischer, 1960; MacArthur, 1975). However, 34 species were unique to northern Sweden and suggests that additional sampling from a broader geographic range will undoubtedly add species to the Alberta list.

A lognormal species distribution model best explains saproxylic beetle distribution from *Populus* CWM (Figure 2-4). However, much controversy exists in the literature pertaining to the value of species distribution models. One explanation of the lognormal distributions fit to biotic communities is simply that it is an artifact of the statistical properties of large numbers, and thus may not have special ecological significance (Preston, 1948; May, 1975; Magurran, 1988). On the other hand, Sugihara (1980) and Pielou (1975) suggest that a lognormal distribution results where resources and niches are randomly and sequentially split by various taxa. In general, the lognormal distribution is usually associated with diverse and variable communities with many resources and interactions among species (Magurran, 1988). Thus, the beetle fauna collected from *Populus* CWM may be a reflection of underlying habitat diversity.

A typical snag or log often contains a mosaic of microhabitats. For instance, more than 250 species of fungi are associated with aspen decay in North America (Lindsey and Gilbertson, 1978). This provides a broad resource base for fungivorous insects, which dominated the beetle fauna from *Populus* CWM (Figure 2-6). Families such as the Leiodidae, Micropeplidae, Staphylinidae, Cerylonidae, Corylophidae and others have species adapted to feed on fungal hyphae, mycelia, spores, and both external and subcortical slime molds (Campbell, 1968; Wheeler and Blackwell, 1984; Peck, 1990). The Ciidae have adapted to feed on conks that form on the trunk (Lawrence, 1971). Fungivores may also partition resources by specializing on particular species of fungi (Jonsell and Nordlander, 1995). It is not known how many of these fungivorous species are specific to *Populus*, but the vast majority are probably generalists and may be associated with fungi in other species of CWM, in soil, and mushrooms (see Palm, 1951,1959).

The beetle community associated with *Populus* CWM is also composed of a large number of predators and scavengers. The relative abundance of scavengers (Figure 2-6) may be an under representation because many predaceous beetles are also opportunists. Nevertheless, the vast majority of predators collected seem to be generalists, belonging to the Carabidae, Staphylinidae, Cucujidae and other ground dwelling and bark inhabiting taxa (Martel et al., 1991; Niemelä et al., 1993). The few specialist predators include taxa from the Rhizophagidae, Histeridae, and Salpingidae.

Phloeophagous, xylophagous, and ambrosia beetles (herein designated as wood borers) are relatively host specific and prefer weakened or recently dead wood. For instance, *Trypodendron retusum* (LeConte) has a symbiotic relationship with ambrosia fungi which are actively cultivated and 'farmed' in their galleries, and is primarily collected from newly dead aspen (Abrahamson, 1967; Wood, 1982; Brewer et al., 1988). However, many other scolytids, buprestids, and cerambycids known to utilize *Populus* in Alberta, were not collected during this study. It may be that decay of most CWM sampled was too advanced for these species. Also, some wood boring species, such as *Saperda,* are known to prefer forest edges (Ives and Wong, 1988), which were not sampled in this study.

Coarse woody material not only provides a direct or indirect food source for insects, but also shelter and overwintering sites. For example, many species of herbivorous beetles in the families Curculionidae and Chrysomelidae, predaceous coccinellids and water beetles in the families Dytiscidae, Hydraenidae and Hydrophilidae were also reared from CWM, and are believed to overwinter in such habitats (Table 2-2) (Belicek, 1976; Smetana, 1988). Thus these species may contribute to the complexity of CWM assemblages through possible interactions with saproxylic species (e.g., as prey, occupying overwintering sites available to other species, etc.).

2.5.3 Comparison of collection methods

All sampling methods have some degree of bias (e.g. Younan and Hain, 1982; Danks et al., 1987; Morrill et al., 1990; Biological Survey of Canada, 1994; Siitonen, 1994; Spence and Niemelä, 1994) and this is true of both methods used in this study. Rearings and window-traps tend to work at two different scales of resolution. Thus, sampling natural variability in CWM faunas depends on method. Rearings give a good estimate of the variation in faunal structure between wood bolts. However, cutting bolts and placing them in cages likely resulted in changes in the environment, largely through an increase in temperature and decreased moisture, which may have adversely affected species requiring cooler and moister conditions typical of the forest. On the other hand, window-traps give estimates of the saproxylic fauna at the stand level. The trap is not intrusive, so the environment is not changed. Window-traps, though, tend to reduce variability across individual snags because they collect species not associated with the particular snag sampled, so that species lists must be carefully screened (Table 2-2).

These methods also have taxon bias. Rearings were efficient at collecting microarthropods such as collembolans, mites, pseudoscorpions, and other groups such as the Psocoptera that are not very vagile (Figure 2-3A). Unfortunately, cutting, handling and transporting samples for rearing probably resulted in loss of vagile species found beneath bark, including many predators such as carabids and staphylinids. Thus, the relative abundance of predators (Table 2-4 and Figure 2-6) collected from rearings likely under-estimates the true number of predators in wood. Window-traps, however, are biased towards species that disperse by flight (Figure 2-3) and seem more reliable in collecting transient groups such as predatory beetles, adult wood borers, and many fungivorous species (Table 2-4).

The biological information provided by each method is also quite different. Data from rearings provides good information on the emergence times of species from CWM and inventory of species utilizing CWM as shelter or for overwintering. Window-traps, like pitfall traps (Spence and Niemelä, 1994), measure arthropod activity and thus resulting data are well suited for measuring seasonal patterns of activity. However, because they can only be attached to snags, logs and other components of CWM are excluded from sampling.

There are also practical considerations. Cutting and rearing of wood bolts is laborious, and only a small number of samples can be reared because of space limitations. Therefore replication is limited. However, window-traps are small, relatively easy to construct, and provide a large number of replicate samples. Some strictly saproxylic species such as *Laemophloeus biguttatus* (Say) and *Dendrophagus cygnaei* Mannerheim were only collected by window-traps (Table 2-2), suggesting that large numbers of window-traps may also provide a 'wider sweep' of the fauna.

Direct comparison of the beetle catches from both trapping methods showed that species distributions tended to be similar among methods (Table 2-3; Figure 2-5), but window-traps collected a significantly higher number of beetles (Table 2-3). Faunal trophic structure, however, was similar between rearings and window-traps (Table 2-4 and Figure 2-6). In addition, 54 species were collected only in rearings, and 96 species were collected only with window-traps (Table 2-2). These data suggest a combination of trapping methods is required to adequately sample the heterogeneity of habitats associated with dead wood, and to sample communities at different spatial scales.

2.5.4 Values and problems of species inventories

Faunal inventories have important applications in community ecology and forest management. Species lists (Tables 2-1 and 2-2), in addition to outlining arthropod faunal structure, provides a baseline for comparison of future studies of the impacts of forest development. The collecting methods proposed offer a relatively simple and cost efficient way to biomonitor insect groups for use in environmental impact assessment, and can be adapted to census insect populations and communities providing community ecologists an opportunity to study forest insect community structure in other forest types.

One problem associated with conducting faunal inventories is the paucity of taxonomic information about Nearctic taxa. This was especially evident with respect to beetles associated with CWM. A large number of taxa could not be identified to specific level, and for others identifications are tentative. The CWM arthropod community is an important ecological group sensitive to forest disturbance (Speight, 1989). However, in order to adequately inventory, monitor, and study ecological requirements of this community, it is necessary to confidently identify the fauna. As taxonomic and systematic support decreases, conservation work will focus on known taxa, while work on unknown and possibly imperiled species receives no support or attention. As availability of taxonomic expertise and investment in systematic biology continues to decline in North America, reliable species level determinations will become more difficult to obtain, making conservation work increasingly difficult (Wilson, 1992). Significant investment is required in arthropod systematics to understand global biodiversity, to ensure preservation of natural processes, and to guide development of environmental policy and practice.

Table 2-1. Arthropod groups (excluding Coleoptera) collected from *Populus* coarse woody material, using rearings from wood bolts and collections from window-traps attached to the boles of snags, 1993-95. Collections were made from aspen-dominated boreal mixedwood stands near Lac la Biche (54° 51' N, 111° 27' W) and Eureka River (56° 35' N, 118° 37' W), Alberta. (Classifcation based on: [a]Danks, 1979; [b]Mc Alpine et al., 1981; [c]Hodges, 1983; [d]Goulet and Huber, 1993).

Class	**Subclass**	**Order**	**Family**	**Species**
[a]Arachnida	Phalangida	Opiliones		not determined
	Chelonethida	Pseudoscorpionida	Chernetidae (?)	*Dendrochernes* (?) spp.
	Labellata	Araneae	Dictynidae	not determined
			Theridiidae	*Steatoda* spp.
			Erigonidae	*Sisicottus montanus* (Emerton)
			Lycosidae	*Pardosa* spp.
				Pirata spp.
			Clubionidae	*Clubiona* spp.
	Acari	Acariformes		not determined
Diplopoda				not determined
Chilopoda				not determined
[a]Collembola		Arthropleona	Poduridae	not determined
			Entomobryidae	not determined
			Isotomidae	not determined
			Hypogastruridae	not determined
		Symphypleona	Sminthuridae	not determined
Insecta	Ptilota	[a]Plecoptera	Capniidae	not determined
		Psocoptera		not determined
		[a]Hemiptera	Saldidae	*Saldula palustris* (Douglas)
			Pentatomidae	*Euschistus servus euschistoides* (Voll.)
				Elasmostethus cruciatus Say
			Lygaeidae	*Peritrechus saskatchewanensis* Barber
				Blissus canadensis (?) Leonard
				Geocoris bullatus (Say)
				Trapezonotus arenarius (L.)
			Aradidae	*Aneurus inconstans* (Uhler)
			Nabidae	*Nabis americoferus* Carayon
			Miridae	*Melanotrichus coagulatus* (Water)
				Chlamydatus pullus (Reuter)
				Lygus borealis (Kelton)
				Lygus lineolaris Palisot de Beauvois

	Anthocoridae	*Anthocoris* spp.
	Cercopidae	*Aphrophora gelida* (Walker)
		Philaenus spumarius (L.)
	Cicadellidae	*Idiocerus musteus* Ball
		Idiocerus pallidus Fitch
		Colladonus youngi Nielson
		Euscelis maculipennis DeLong & Davidson
		Commellus sexvittabus (VanDuzee)
		Diplocolenus evansi (Ashmead)
		Sorhoanus orientalis (DeLong & Davidson)
		Sorhoanus uhleri (Oman)
		Empoasca gelbata (DeLong & Davidson)
		Empoasca sp.
		Psammotettix lividellus (Zetterstedt)
		Oncopsis albicollis Hamilton
		Draeculacephala manitobiana Ball
	Fulgoridae	*Epiptera pallida* (Say)
		Liburnia spp.
[a]Thysanoptera	Thripidae	not determined
[b]Diptera	Tipulidae	not determined
	Bibionidae	not determined
	Sciaridae	not determined
	Mycetophilidae	not determined
	Cecidomyiidae	not determined
	Psychodidae	not determined
	Synneuridae	*Synneuron decipiens* Hutson
	Culicidae	not determined
	Ceratopogonidae	not determined
	Chironomidae	not determined
	Asilidae	not determined
	Empididae	not determined
	Dolichopodidae	not determined
	Phoridae	not determined
	Micropezidae	not determined
	Neriidae	not determined
	Syrphidae	not determined
	Clusiidae	not determined
	Heleomyzidae	not determined

	Sphaeroceridae	not determined
	Anthomyiidae	not determined
	Muscidae	not determined
[c]Lepidoptera	Gracillariidae	*Phyllonorycter* spp.
	Oecophoridae	*Bibarrambla allenella* Wlsm.
	Gelechiidae	*Filatema* spp.
		Gelechia spp.
		Chionodes spp.
		Neotelphusa spp.
	Tortricidae	*Choristoneura conflictana* Walker
	Arctiidae	*Euxoa ochragaster* (Guenee)
		Euxia tessellata (Walker)
		Protolampra rufipectus (Morrison)
		Aplectoides condita (Guenee)
	Noctuidae	*Apamea commoda* (Walker)
		Apamea devastator (Brace)
		Spaelotis clandestina (Harris)
[d]Hymenoptera	Cimbicidae	*Zaraea inflata* Norton
	Tenthredinidae	*Doleris neocollaris* MacGilliuray
		Pristiphora pallipes Lepeletier
	Sphecidae	*Passalaecus* spp.
	Formicidae	*Camponotus herculeanus* (L.)
		Formica rufa fossceps Buren
		Formica neorufibaris Emery
		Formica fusca L.
		Myrmica 2 sp.
	Encyrtidae	*Copidosoma* 2 sp.
		Tyndarichus spp.
		Encyrtidae sp.
	Eulophidae	*Euplectrus* spp.
		Chrysocharis spp.
		Melittobia spp.
		Pediobius spp.
	Eurytomidae	*Tetramesa* spp.
	Mymaridae	*Anaphes* spp.
		Polynema spp.
	Pteromalidae	*Habritys brevicornis* (Ratzeburg)
		Coelopisthia spp.

	Gastrancistrus spp.
Torymidae	*Torymus* spp.
Charipidae	*Phaenoglyphis americana* Baker
Aphidiidae	Aphidiidae 2 sp.
	Aphidius spp.
Braconidae	*Dacnusa* spp.
	Phaenocarpa 2 sp.
	Blacus spp.
	Bracon spp.
	Chelonus spp.
	Spathius spp.
	Heterospilus spp.
	Meteorus 2 sp.
	Cantharoctonus spp.
	Cotesia spp.
	Apanteles spp.
	Micropletus spp.
	Aleoides spp.
Ichneumonidae	Ichneumonidae 3 sp.
	Gelis spp
	Endasys spp.
	Mesoleptidea spp.
	Diplazon laetatorius Fabricius
	Orthocentrus spp.
	Scambus tecumseh Vieneek.
	Odontocolon 2 sp.
Ceraphronidae	*Ceraphron* spp.
Gasteruptiidae	*Gasteruption assectator* L.
Platygastridae	*Platygaster* spp.
	Synopeas spp.
Scelionidae	*Telenomus* 5 sp.
	Trimorus 6 sp.
Diapriidae	*Spilomicrus inornatus* Masner
	Basalys spp.
	Monelata cincta (Hal.)
	Zygota spp.
	Polypeza spp.

Table 2-2. Coleoptera collected from *Populus* coarse woody material in aspen dominated boreal-mixedwood stands near Lac la Biche (54° 51' N, 111° 27' W) and Eureka River (56° 35' N, 118° 37' W), Alberta. Beetles were collected using a combination of rearing from wood bolts (1993-94) and modified window-traps attached to the boles of snags (1994-95).

([a]LLB=Lac la Biche, ER=Eureka River; [b]R=rearing, W=window-trap, B=both methods; [c]F=fungivore, P=predator, WB=wood borer, S=scavenger, ?=unknown or uncertain of the stage(s) found in dead wood; †=taxa not considered saproxylic and not included in analysis; ††=saproxylic, but not known from *Populus* in Alberta, and not included in analysis; NR=new provincial record according to Bousquet (1991)).

Family	Species	Year collected	Place[a]	Method[b]	Role[c]
Aderidae	NR *Aderus populneus* (Panzer)	94	LLB	R	?
Anobiidae	*Caenocara scymnoides* LeConte	93/94	ER	B	WB
	Hemicoelus carinatus (Say)	93/94/95	B	B	WB
	Ptilinus lobatus Casey	93/94/95	B	B	WB
	Tricorynus densus (Fall)	94/95	B	W	WB
	Utobium elegans (Horn)	94	B	W	WB
	NR *Xestobium marginicolle* (LeConte)	94/95	ER	W	WB
Anthicidae	*Anthicus ancilla* Casey	93	ER	R	S
	Anthicus cervinus LaFerte-Senectere	93	ER	R	S
	Anthicus coracinus LeConte	93/94	B	B	S
	Anthicus hastatus Casey	93	LLB	R	S
Anthribidae	*Allandrus populi* Pierce	93/94/95	B	B	F
Apionidae	† *Apion centrale* Fall	93/94	B	B	H
Bostrichidae	NR *Endecatomus rugosus* (Randall)	95	LLB	W	WB
Buprestidae	*Agrilus liragus* Bart.&Brn.	93/94/95	B	B	WB
	†† *Anthaxia aenogaster* Cast.&Gory	94	ER	R	WB
	Dicerca tenebrica (Kirby)	93/94	B	B	WB
Byturidae	† *Byturus unicolor* Say	95	ER	W	H
Cantharidae	*Podabrus* spp.	93/94/95	B	B	P
	Silis difficilis LeConte	94	ER	W	P
Carabidae	*Agonum placidum* (Say)	93	B	R	P
	Agonum retractum LeConte	94/95	LLB	W	P
	Agonum sordens Kirby	93/95	B	B	P
	Amara apricaria Paykull	93/94/95	LLB	R	P
	Amara confusa LeConte	93	LLB	R	P
	Amara cupreolata Putzeys	93/94	LLB	R	P
	Amara idahoana (Casey)	94/95	ER	W	P
	Amara lacustris LeConte	94	B	B	P
	Amara latior (Kirby)	93/94	LLB	B	P

		Amara pallipes Kirby	93	ER	R	P
		Amara sinuoasa (Casey)	94	LLB	R	P
		Bembidion spp.	93/94/95	B	B	P
		Bradycellus lecontei Csiki	94/95	LLB	B	P
		Bradycellus nigrinus Dejean	95	ER	W	P
		Calathus ingratus Dejean	94/95	B	W	P
		Calosoma frigidum Kirby	94/95	B	W	P
		Dyschirius interior Fall	94	LLB	W	P
		Dyschirius longulus LeConte	93	LLB	R	P
		Platynus decentis (Say)	93/94/95	B	B	P
		Pterostichus adstrictus Escholtz	94/95	LLB	W	P
		Pterostichus pensylvanicus LeConte	95	LLB	W	P
		Pterostichus punctatissimus (Randall)	95	LLB	W	P
		Stenolophus conjunctus (Say)	93/94/95	B	B	P
		Syntomus americana Dejean	94/95	LLB	W	P
		Trichocellus cognatus (Gyllenhal)	93/94/95	B	B	P
Cephaloidae		*Cephaloon tenuicorne* LeConte	94/95	B	W	WB
Cerambycidae	NR	*Bellamira scalaris* (Say)	94	LLB	W	WB
	††	*Elatotrypes hoferi* Fisher	94	LLB	W	WB
		Grammoptera subargentata (Kirby)	94/95	B	B	WB
		Hyperplatys aspersa (Say)	93/95	LLB	B	WB
		Judolia montivagens (Couper)	94/95	B	W	WB
	††	*Pogonocherus mixtus* Haldeman	93/94/95	B	W	WB
	††	*Pogonocherus parvulus* LeConte	93/94/95	B	W	WB
		Trachysida mutabilis (Newman)	93/94/95	B	B	WB
	††	*Xylotrechus annosus* (Say)	95	LLB	W	WB
	††	*Xylotrechus undulatus* (Say)	93/94	ER	R	WB
Cerylonidae		*Cerylon castaneum* Say	93/94/95	B	B	F
Chrysomelidae	†	*Chaetocnema protensa* LeConte	93	LLB	R	H
	†	*Chrysomela crotchi* Brown	93/94/95	LLB	W	H
	†	*Chrysomela falsa* Brown	94	LLB	W	H
	†	*Chrysomela mainensis* Brown	94	LLB	W	H
	†	*Crepidodera nana* (Say)	94	ER	W	H
	†	*Distigmoptera borealis* Blake	93/94	B	B	H
	†	*Orsodacne atra* (Ahrens)	93/94/95	B	B	H
	†	*Phaedon armoraciae* (L.)	93	LLB	R	H
	†	*Phratora purpurea* Brown	94	LLB	W	H
	†	*Phyllotreta pusilla* Horn	93	B	R	H
	†	*Phyllotreta robusta* LeConte	93	LLB	R	H
	†	*Phyllotreta striolata* (Fabricius)	93	LLB	R	H

	† *Psylliodes punctulata* Melsheimer	93/94	B	R	H
	† *Syneta hamata* Horn	93/94	LLB	W	H
	† *Syneta pillosa* Brown	95	LLB	W	H
	† *Trirhabda borealis* Blake	95	LLB	W	H
	† *Zeugophora abnormis* (LeConte)	94	ER	W	H
Ciidae	*Cis americanus* Mannerheim	93/94/95	B	B	F
	Cis fuscipes Mellie	94	B	W	F
	Cis levettei (Casey)	94/95	LLB	W	F
	Cis pistorius Casey	94	LLB	R	F
	Dolichocis manitoba Dury	93/94/95	B	B	F
	Orthocis punctatus (Mellie)	93/94/95	B	B	F
	Sulcacis curtula (Casey)	93/94/95	B	B	F
Clambidae	*Clambus pubescens* Redtenbacher	94/95	B	W	F
Coccinellidae	† *Adalia bipunctata* (L.)	93	LLB	R	P
	† *Calvia quatuordecimguttata* (L.)	94/95	LLB	B	P
	† *Coccinella prolongata* Crotch	94	B	B	P
	† *Coccinella trifasciata* Mulsant	94	ER	W	P
	† *Hippodamia parenthesis* (Say)	93	ER	R	P
	† *Hippodamia tredecimpunctata* (Say)	93	LLB	R	P
	† *Macronaemia episcopalis* (Kirby)	93	ER	R	P
	† *Mulsantina hudsonica* (Casey)	93/94	B	B	P
	Psyllobora vigintimaculata (Say)	93/94/95	LLB	B	F
	Scymnus spp.	94/95	B	W	P
Corylophidae	*Molamba biguttata* (LeConte)	93/94/95	B	B	F
	Orthoperus scutellaris LeConte	93/94/95	B	B	F
Cryptophagidae	*Atomaria (Anchicera) ephippiata* Zimmerman	93/94/95	B	B	F
	Atomaria (Anchicera) spp.	93/94/95	B	B	F
	Atomaria (Atomaria) spp.	93/94/95	B	B	F
	Antherophagus ochraceus Melsheimer	94/95	B	W	F
	Caenoscelis spp.	94/95	B	B	F
	Cryptophagus acutangulus Gyllenhal	93/94/95	B	B	F
	Cryptophagus laticollis Lucas	93/94	B	B	F
	Cryptophagus tuberculosis Maklin	94/95	B	W	F
	Henoticus spp.	93/94/95	B	B	F
Cucujidae	*Cucujus clavipes* Fabricius	93/94/95	B	B	P
	Dendrophagus cygnaei Mannerheim	94	B	W	P
	NR *Laemophloeus biguttatus* (Say)	94/95	LLB	W	P
	Pediacus fuscus Erichson	94/95	LLB	W	P
Curculionidae	† *Ceutorhynchus punctiger* Gyllenhal	94/95	B	B	H
	Cossonus pacificus VanDyke	93/94/95	B	B	WB

		Cryptorhynchus lapathi (L.)	93/95	B	B	WB
	†	*Dorytomus laticollis* LeConte	94/95	B	W	H
	†NR	*Dorytomus lecontei* O'Brien	95	LLB	W	H
	†	*Elleschus* spp.	94/95	ER	B	H
	†	*Lepyrus oregonus* VanDyke	94/95	B	W	H
	†	*Listronotus maculicollis* (Kirby)	93	ER	R	H
	††	*Magdalis gentilis* LeConte	94/95	B	W	WB
	††	*Magdalis subtincta* LeConte	94/95	B	B	WB
	†	*Notaris bimaculatus* (Fabricius)	93	B	R	H
	†	*Notaris puncticollis* (LeConte)	93	LLB	R	H
	†	*Otiorhynchus ovatus* (L.)	93/94/95	B	B	H
		Phloeophagus canadensis VanDyke	93/94/95	B	B	WB
	†	*Proctorus armatus* LeConte	95	LLB	W	H
		Rhyncolus brunneus Mannerheim	93/95	B	B	WB
	NR	*Rhyncolus knowltoni* (Thatcher)	93/94	ER	R	WB
	†NR	*Rhyncolus macrops* Buchanan	94	ER	W	WB
	†	*Sitona cylindricollis* (Fahraeus)	93	B	B	H
	†	*Sitona lineelus* (Bonsd.)	93/94/95	B	B	H
	†	*Tanysphyrus lemnae* (Fabricius)	94/95	B	B	H
	†	*Tychius picirostris* (Fabricius)	93/94	B	B	H
Dermestidae		*Dermestes caninus* Germar	94	LLB	W	S
		Dermestes lardarius L.	93/94/95	B	B	S
		Trogoderma sinistrum Fall	93/94/95	B	B	S
Dytiscidae	†	*Agabus* spp.	94	LLB	W	P
	†	*Laccornis pacificus* Leech	94	LLB	R	P
Elateridae		*Ampedus apicatus* (Say)	93/94/95	B	B	P
		Ampedus deletus (LeConte)	93/94/95	B	B	S
		Ampedus luctuosis (LeConte)	94/95	B	W	S
	†	*Ampedus miniipennis* (LeConte)	94/95	B	W	S
		Ampedus mixtus (Herbst)	93/94/95	B	B	S
	NR	*Athous productus* (Randall)	93	LLB	R	S
	†	*Ctenicera arata* (LeConte)	93	LLB	R	S
	†	*Ctenicera hoppingi* (VanDyke)	94	B	W	S
	†	*Ctenicera lutescens* (Fall)	95	B	W	S
	†	*Ctenicera mendax* (LeConte)	94/95	B	W	S
	†	*Ctenicera nitidula* (LeConte)	94/95	B	W	S
	†	*Ctenicera propola* (LeConte)	94/95	B	W	S
		Ctenicera resplendens (Escholtz)	94/95	B	W	S
	†	*Ctenicera stricklandi* (Brown)	94/95	B	W	S
	†	*Ctenicera triundulata* (Randall)	94/94	B	W	S

		Denticollis denticornis (Kirby)	93/94	B	B	S
	†	*Drasterius debilis* LeConte	94/95	B	W	S
	†	*Eanus decoratus* Mannerheim	94/95	B	W	S
	†	*Eanus estriatus* (LeConte)	95	ER	W	S
	††NR	*Harminius triundulatus* (Mannerheim)	95	ER	W	S
	†	*Hypnoidus bicolor* (Escholtz)	95	ER	W	H
		Megapenthes stigmosus (LeConte)	94/95	LLB	W	S
Endomychidae		*Lycoperdina ferruginea* LeConte	95	LLB	W	F
Erotylidae	NR	*Dacne* (?) *californica* (Horn)	94/95	B	B	F
		Triplax (?) *californica* LeConte	94/95	B	B	F
Eucinetidae		*Eucinetus punctulatus* LeConte	94/95	B	W	F
Eucnemidae	NR	*Dirhagus pectinatus* (LeConte)	94/95	B	W	?
	NR	*Epiphanis cornutus* Escholtz	93/94/95	B	B	?
		Hylis terminalis (LeConte)	94/95	LLB	W	?
Heteroceridae	†	*Heterocerus* spp.	93	LLB	R	S
Histeridae	NR	*Abraeus bolteri* LeConte	94/95	B	W	P
		Paramalus bistriatus Erichson	94/95	B	B	P
		Platysoma lecontei Marseul	94/95	B	B	P
	NR	*Teretrius montanus* Horn	94/95	B	B	P
Hydraenidae	†	*Ochthebius* spp.	93	LLB	R	S
Hydrophilidae		*Cercyon cinctus* Smetana	93/94/95	B	B	S
		Cercyon pygmaeus (Illiger)	94/95	B	B	S
	†	*Enochrus hamiltoni* (Horn)	93	LLB	R	S
	†	*Helophorus orientalis* Motschulsky	93	B	R	S
	†	*Hydrochara obtusata* (Say)	95	ER	W	S
	†NR	*Hydrochus granulatus* Blatcheley	94	LLB	R	S
Lampyridae	NR	*Ellychnia corrusca* (L.)	94/95	LLB	W	P
		Pyractomena borealis (Randall)	93/94/95	LLB	B	P
Lathridiidae		*Cartodere constricta* (Gyllenhal)	93/94/95	B	B	F
		Corticaria spA	93/94/95	B	B	F
		Corticaria spB	93/94/95	B	W	F
		Corticaria spC	93/94/95	B	W	F
		Corticaria spD	93/94/95	B	B	F
		Corticaria spE	93/94/95	B	B	F
		Corticaria spF	93/94/95	B	B	F
		Corticarina spp.	93/94/95	B	B	F
		Cortinicara gibbosa (Herbst)	93/94/95	B	B	F
		Enicmus spA	93/94/95	B	B	F
		Enicmus spB	93/94/95	B	B	F
		Enicmus spC	93/94/95	B	W	F

		Lathridius spA	93/94/95	B	B	F
		Lathridius spB	93/94/95	B	B	F
	NR	*Melanopthalma pumilla* (LeConte)	93/94/95	B	B	F
	NR	*Melanopthalma villosa* (Zimmerman)	93/94/95	B	B	F
Leiodidae		*Agathidium* spp. (=?*depressum* Fall)	93/94/95	B	B	F
		Anisotoma globososa Hatch	94/95	B	B	F
	NR	*Anisotoma horni* Wheeler	94	LLB	W	F
		Anisotoma spp. (= ?*errans* Brown)	93/94/95	B	W	F
		Anogdus spp.	93/94	B	B	F
		Catop alsiosus (Horn)	94	LLB	W	S
		Catops americanus Hatch	94/95	B	W	S
		Catops basilaris Say	94/95	B	W	S
		Colon spp.	94	ER	W	F
		Hydnobius spp.	94	ER	W	F
		Leiodes spp.	94	ER	W	F
Lucanidae		*Platycerus piceus* (Kirby)	95	ER	W	S
Lycidae		*Dictyopterus thoracicus* (Randall)	95	ER	R	P
Lyctidae	NR	*Lyctus planicollis* LeConte	94/95	B	W	WB
Lymexylidae		*Hylecoetus lugubris* Say	94/95	B	B	WB
Melandryidae		*Dircaea liturata* (LeConte)	95	B	W	S
		Enchodes sericea (Haldeman)	93/94/95	B	B	S
	NR	*Hallomenus scapularis* Melsheimer	93/94	ER	R	S
		Melandrya striata Say	93/94/95	B	B	S
	NR	*Orchesia castanea* (Melsheimer)	94/95	LLB	B	S
		Phryganophilus collaris LeConte	95	LLB	W	S
		Zilora hispida LeConte	94/95	B	B	S
Melyridae	†	*Malachius* spp.	94/95	LLB	B	P
Micropeplidae		*Micropeplus laticollis* Maklin	94	ER	W	F
Mordellidae	†	*Mordellistena scapularis* (Say)	94	LLB	W	H
Mycetophagidae		*Mycetophagus distinctus* Hatch	93/94/95	B	B	F
		Mycetophagus pluripunctatus LeConte	94/95	LLB	W	F
Nitidulidae		*Colopterus truncatus* (Randall)	93/94/95	ER	B	F
		Epuraea spp.	93/94/95	B	B	F
		Glischrochilus moratus Brown	93/94/95	B	B	F
		Glischrochilus quadrisignatus (Say)	94/95	B	B	F
		Glischrochilus sanguinolentus (Olivier)	93/94	B	W	F
		Glischrochilus siepmanni Brown	93/94/95	B	B	F
	†	*Nitidula ziczac* Say	93/94	B	W	S
Phalacridae	†NR	*Phalacrus penicillatus* (Say)	94	LLB	R	H
Pselaphidae		*Actium* spp.	93/94	ER	R	P

		Batrisodes spp. (=? *frontalis* (LeConte))	93/94/95	B	B	P
	NR	*Euplectus duryi* Casey	93/94/95	LLB	B	P
Ptiliidae	NR	*Acrotrichus* spp.	93/94/95	B	B	F
		Ptiliidae spp.	93/94	B	B	F
Pyrochroidae		*Dendroides testaceus* LeConte	93/94/95	B	B	F
		Schizotus cervicalis Newman	93/94	B	B	F
Pythidae	††	*Priognathus monilicornis* (Randall)	94	ER	W	WB
Rhipiphoridae	NR	*Pelecotoma flavipes* Melsheimer	93/94/95	LLB	B	?
Rhizophagidae		*Monotoma picipes* Herbst	94/95	B	W	F
		Rhizophagus dimidiatus Mannerheim	94	ER	R	P
		Rhizophagus bruneus Horn	93/94/95	B	B	P
		Rhizophagus remotus LeConte	93/94/95	B	B	P
Salpingidae	NR	*Rhinosimus viridiaeneus* Randall	94	LLB	W	P
		Sphaeriestes virescens (LeConte)	93/94/95	B	B	P
Scaphidiidae	NR	*Baeocera* spp.	93	B	R	F
Scarabaeidae	†	*Aphodius bidentatus* Schmidt	94	LLB	W	S
	†	*Aphodius distinctus* Muller	93/94/95	B	B	S
	†	*Aphodius fimetarius* L.	94/95	B	B	S
	†	*Aphodius hyperboreus* LeConte	94	ER	W	S
	†	*Onthophagus hecate* (Panzer)	93/94	LLB	B	S
Scirtidae	†	*Cyphon variabilis* (Thunberg)	93/94/95	B	B	S
	†	*Scirtes* (?)*tibialis* Guerin-Meneville	94/95	B	W	S
Scolytidae	††	*Dendroctonus punctatus* LeConte	95	ER	W	WB
	††	*Phloeosinus pini* Swaine	95	ER	W	WB
	††	*Pityophthorus* (?)*tuberculatus* Eichhoff	93/94/95	B	B	WB
	††	*Polygraphus rufipennis* (Kirby)	95	B	W	WB
		Procryphalus mucronatus (LeConte)	93/94/95	B	B	WB
		Trypodendron retusum (LeConte)	93/94/95	B	B	WB
Scraptiidae		*Anaspis rufa* Say	94	ER	W	?
	NR	*Canifa pallipes* (Melsheimer)	93/94/95	B	B	?
Scydmaenidae	NR	*Stenichnus* (?)*ovipennis* (Casey)	93/94	LLB	B	P
Sphindidae		*Sphindus americanus* LeConte	95	LLB	W	F
Staphylinidae		*Acidota crenata* (Fabricius)	94/95	B	W	P
		Acidota quadrata (Zetterstedt)	94	ER	W	P
		Aleocharine spp.	93/94/95	B	B	?
	NR	*Anomognathus* spp.	93/94	B	B	P
	NR	*Anotylus rugosus* (Fabricius)	93	LLB	R	S
		Anotylus sobrinus (LeConte)	93/94	B	B	S
		Atrechus macrocephalus (Nordm.)	93	LLB	R	P
		Bledius gravidus Casey	93	ER	R	S

	Bledius strenuus Casey	93	ER	R	S
	Bolitopunctus muricatulus (Hatch)	95	ER	W	P
NR	*Bryophacis smetanai* Campbell	95	LLB	W	P
NR	*Bryoporus rufescens* LeConte	93	B	R	P
NR	*Carpelimus* sp A	93/94	B	R	S
NR	*Carpelimus* sp B	93	ER	R	S
NR	*Carphacis nepigonensis* (Bernhauer)	93/94/95	B	B	P
	Coproporus ventriculus (Say)	94/95	B	B	S
	Cypha crotchi Horn	93	LLB	R	P
NR	*Elonium diffusum* (Fauvel)	93	LLB	R	S
	Eusphalerum fenyesi (Bernhauer)	94	LLB	W	?
	Gabrius brevipennis (Horn)	93/94	LLB	B	P
	Hapalaraea floralis (Paykull)	93	LLB	R	P
NR	*Hapalaraea hamata* (Fauvel) (=*Elonium barri* Hatc	94	B	W	S
NR	*Heterothops fusculus* LeConte	94	LLB	W	P
	Heterothops pusio LeConte	93	LLB	R	P
NR	*Homalota* spp.	93	ER	R	P
	Lathrobium fauveli Duvivier	93/94	B	B	P
	Lathrobium fulvipenne Gravenhorst	93	LLB	R	P
	Lordithon bimaculatus (Couper)	94/95	LLB	B	P
	Lordithcn fungicola Campbell	94/95	B	W	P
	Lordithon longiceps (LeConte)	94/95	B	W	P
	Lordithon thoracicus (Fabricius)	94/95	ER	W	P
NR	*Mycetoporus americanus* Erichson	93/94	B	W	P
NR	*Mycetoporus brunneus* Marsh.	93	ER	R	P
	Mycetoporus splendidus (Gravenhorst)	94	B	W	P
	Neohypnus obscurus (Erichson)	93/94	B	R	P
	Nudobius cephalus (Say)	93/94/95	B	B	P
	Olisthaerus megacephalus (Zetterstedt)	93/94/95	B	B	P
	Ontholestes cingulatus (Gravenhorst)	94	LLB	W	P
	Oxyporus occipitalis Fauvel	95	ER	W	F
	Philonthus concinnis (Gravenhorst)	93	LLB	R	P
	Philonthus crestonensis Hatch	94	ER	W	P
	Philonthus cyanipennis (Fabricius)	94/95	B	W	P
	Philonthus occidentalis Horn	93	LLB	R	P
NR	*Philonthus picicornis* Horn	93/94	B	B	P
NR	*Philonthus pugetensis* Hatch	93	LLB	R	P
NR	*Philonthus varians* (Paykull)	93	LLB	R	P
NR	*Philonthus varius* Gravenhorst	93	LLB	R	P
	Phloeonomus lapponicus (Zetterstedt)	93	B	R	S

		Platystethus americanus Erichson	93/94	B	B	S
	NR	*Proteinus limbatus* Maklin	94	LLB	W	?
		Pseudopsis sagitta Herman	93/94	LLB	B	P
		Quedius caseyi Scheerp.	94	ER	W	P
		Quedius criddlei (Casey)	94	B	B	P
		Quedius fulvicollis (Stephens)	94	LLB	R	P
		Quedius plagiatus Mannerheim	93/94/95	B	B	P
		Quedius rusticus Smetana	93/94/95	B	B	P
		Quedius simulator Smetana	93/94	B	B	P
		Quedius velox Smetana	93/94/95	B	B	P
		Sepedophilus littoreus (L.)	93	LLB	R	F
		Sepedophilus testaceus (Fabricius)	93/94	B	B	P
		Siagonium punctatum LeConte	94/95	B	W	S
		Staphylinus pleuralis LeConte	95	B	W	P
		Stenus dolosus Casey	93	ER	R	P
		Stenus immarginatus Maklin	94	LLB	W	P
		Stenus pinguis (Casey)	94	LLB	B	P
		Tachinus basalis Erichson	95	LLB	W	P
		Tachinus elongatus Gyllenhal	93/94/95	B	W	P
		Tachinus frigidus Erichson	94	ER	W	F
		Tachinus fumipennis (Say)	94	B	W	P
		Tachyporus borealis Campbell	93/94	LLB	B	P
		Tachyporus inornatus Campbell	93	LLB	R	P
		Tachyporus maculicollis LeConte	95	B	W	P
		Tachyporus mexicanus Sharp	93/94/95	B	B	P
		Tachyporus nimbicola Campbell	95	B	W	P
		Tachyporus nitidulus (Fabricius)	93/94	B	R	P
		Tachyporus rulomus Blackweld	94	B	R	P
Tenebrionidae		*Bius estriatus* (LeConte)	93/94/95	B	B	F
	NR	*Mycetochara fraterna* (Say)	94/95	LLB	W	F
		Platydema americanum Cast.&Brul.	94/95	B	B	F
		Scaphidema aeneolum (LeConte)	93/94	B	B	F
		Upis ceramboides (L.)	93/94/95	B	B	F
Trogossitidae		*Ostoma ferruginea* (L.)	94	B	W	P
		Tenebroides mauritanicus (L.)	93/94	B	B	P
		Thymalus marginicollis Chevrolat	93/94/95	B	B	P

Table 2-3. Summary of the number of beetle species and their abundance, by family, from collections made by rearings from *Populus* coarse woody material and window-traps attached to snags, in boreal mixedwood forest stands in north-central Alberta. Insect rearings were conducted during the snow-free months of 1993 and 1994. Window-trap sampling was conducted from May to October 1994, and May through August, 1995. See text for details of each analysis. († denotes families not included in Chi-square analysis because of expected values less than 1).

	Number of species			**Standardized abundance**		
Family	**Rearings**	**Window-traps**	**Both methods**	**Rearings**	**Window-traps**	**Both methods**
†Aderidae	1	0	0	2.20	0.00	0.00
Anobiidae	3	6	3	246.53	2833.84	2006.17
Anthicidae	4	1	1	56.71	12.99	17.28
†Anthribidae	1	1	1	36.32	9.01	45.33
†Bostrichidae	0	1	0	0.00	9.80	0.00
Buprestidae	2	2	2	12.48	124.06	136.55
†Cantharidae	0	2	0	0.00	201.90	0.00
Carabidae	15	17	7	259.08	5759.56	4486.95
†Cephaloidae	0	1	0	0.00	155.09	0.00
Cerambycidae	3	4	2	19.15	726.23	729.36
†Cerylonidae	1	1	1	255.25	843.06	1098.30
Ciidae	4	5	2	429.04	207.27	401.69
†Clambidae	0	1	0	0.00	74.01	0.00
Coccinellidae	1	2	1	22.93	146.80	49.02
Corylophidae	2	2	2	744.04	912.21	1656.24
Cryptophagidae	7	9	7	667.09	2092.27	1497.48
Cucujidae	1	4	1	109.35	470.81	553.75
Curculionidae	5	2	2	235.44	1233.81	1268.55
Dermestidae	2	3	2	66.14	182.03	241.68
Elateridae	4	7	3	84.46	863.27	666.21
†Endomychidae	0	1	0	0.00	9.80	0.00
Erotylidae	1	2	1	6.59	2172.22	2155.58
†Eucinetidae	1	1	1	10.05	98.83	108.88
Eucnemidae	1	3	1	20.22	188.65	95.81
Histeridae	3	4	3	17.30	237.21	247.80
Hydrophilidae	2	2	2	52.78	55.64	108.42
Lampyridae	1	2	1	2.81	48.76	35.28
Lathridiidae	12	15	11	1392.56	15963.44	10477.81
Leiodidae	3	11	3	94.93	1704.62	1623.34
†Lucanidae	0	1	0	0.00	9.01	0.00
†Lycidae	0	1	0	0.00	6.71	0.00
†Lyctidae	0	1	0	0.00	644.84	0.00
†Lymexylidae	1	1	1	2.20	185.49	187.69
Melandryidae	5	6	4	138.88	1911.10	2008.31
†Micropeplidae	0	1	0	0.00	13.42	0.00
Mycetophagidae	1	2	1	34.59	194.34	183.24
Nitidulidae	5	5	4	232.30	3053.72	3248.99
Pselaphidae	2	3	2	14.49	138.99	137.75
Ptiliidae	2	2	2	172.63	314.82	487.45
Pyrochroidae	2	2	2	76.52	196.33	272.84
†Rhipiphoridae	1	1	1	39.48	9.80	49.28
Rhizophagidae	3	3	2	742.32	7767.30	8497.03
Salpingidae	1	2	1	7.09	47.97	16.10
†Scaphidiidae	1	0	0	51.66	0.00	0.00
Scolytidae	2	2	2	1115.37	1890.79	3006.15
Scraptiidae	1	2	1	64.08	281.37	325.32
†Scydmaenidae	1	1	1	4.48	6.49	10.97
†Sphindidae	0	1	0	0.00	45.69	0.00
Staphylinidae	48	47	19	3118.91	6611.39	8154.29
Tenebrionidae	3	5	3	48.53	589.26	129.48
Trogossitidae	2	3	2	33.67	253.29	255.74
Grand Total	161	204	108	10740.6	61509.284	56678.071

Table 2-4. Summary of trophic structure from collections made by rearings from *Populus* coarse woody material and window-traps attached to snags, in boreal mixedwood stands in north-central Alberta. Insect rearings were conducted during the snow-free months of 1993 and 1994. Window-trap sampling was conducted from May to October 1994, and May through August, 1995.

	Number of species			Mean standardized abundance		
Trophic Role	**Rearings**	**Window-traps**	**Both methods**	**Rearings**	**Window-traps**	**Both methods**
Unknown	8	13	7	2521.71	4557.44	6886.66
Fungivore	50	69	43	4285.40	28507.08	23494.50
Predator	67	82	38	1788.90	19418.36	18027.99
Scavenger	20	20	8	513.45	1222.46	934.47
Wood borer	16	20	12	1631.16	7803.95	7334.46
Total	161	204	108	10740.62	61509.28	56678.07

Table 2-5. Summary of the number of beetle species collected, by family, from *Populus* coarse woody material sampled from boreal mixedwood forests in north-central Alberta, and 16 sites in middle and southern Sweden (Palm, 1959). († denotes families not included in analysis due to expected values less than 1; [a]excludes the Aleocharinae).

	Number of species	
Family	**Alberta**	**Sweden**
Aderidae	1	2
Anobiidae	6	4
†Anthribidae	2	0
†Aspidophoridae	0	1
†Bostrychidae	1	0
Buprestidae	2	3
†Cantharidae	2	0
Carabidae	18	5
Cerambycidae	6	15
Ciidae	7	13
Cleridae	0	4
Coccinellidae	2	2
Colydiidae	0	7
Corylophidae	2	3
Cryptophagidae	9	19
Cucujidae	4	5
Curculionidae	5	7
Dermestidae	3	3
Elateridae	10	14
Endomychidae	2	4
Erotylidae	2	6
Eucenemidae	3	2
Histeridae	4	10
Lathridiidae	17	22
Leiodidae	14	12
Lucanidae	1	2
†Lycidae	1	1
†Lyctidae	1	0
†Lymexylidae	1	1
Melandryidae	7	9
Melyridae (=Dasytetidae)	0	3
Mordellidae	0	3
Mycetophagidae	2	4
Nitidulidae	8	14
Pselaphidae	4	14
Ptiliidae	2	6
Ptinidae	0	3
Pyrochroidae	2	2
†Rhipiphoridae	1	0
Rhizophagidae	4	5
Salpingidae	2	2
Scaphidiidae	1	5
†Scarabaeidae	0	2
Scolytidae	2	5
†Scraptiidae	2	0
Scydmaenidae	1	6
†Silphidae	0	1
†Sphinididae	1	0
[a]Staphylinidae	79	30
Tenebrionidae	5	7
Trogossitidae	3	5
	252	293

Table 2-6. A comparison of trophic structure of beetle species collected (excluding Aleocharinae and Ptiliidae) from *Populus* coarse woody material sampled from boreal-mixedwood stands in north-central Alberta; and 16 sites in middle and southern Sweden (from Palm, 1959).

	Number of species	
Trophic Role	**Alberta**	**Sweden**
Unknown	14	0
Fungivore	74	101
Predator	111	83
Scavenger	31	40
Wood borer	24	43
Total	254	267

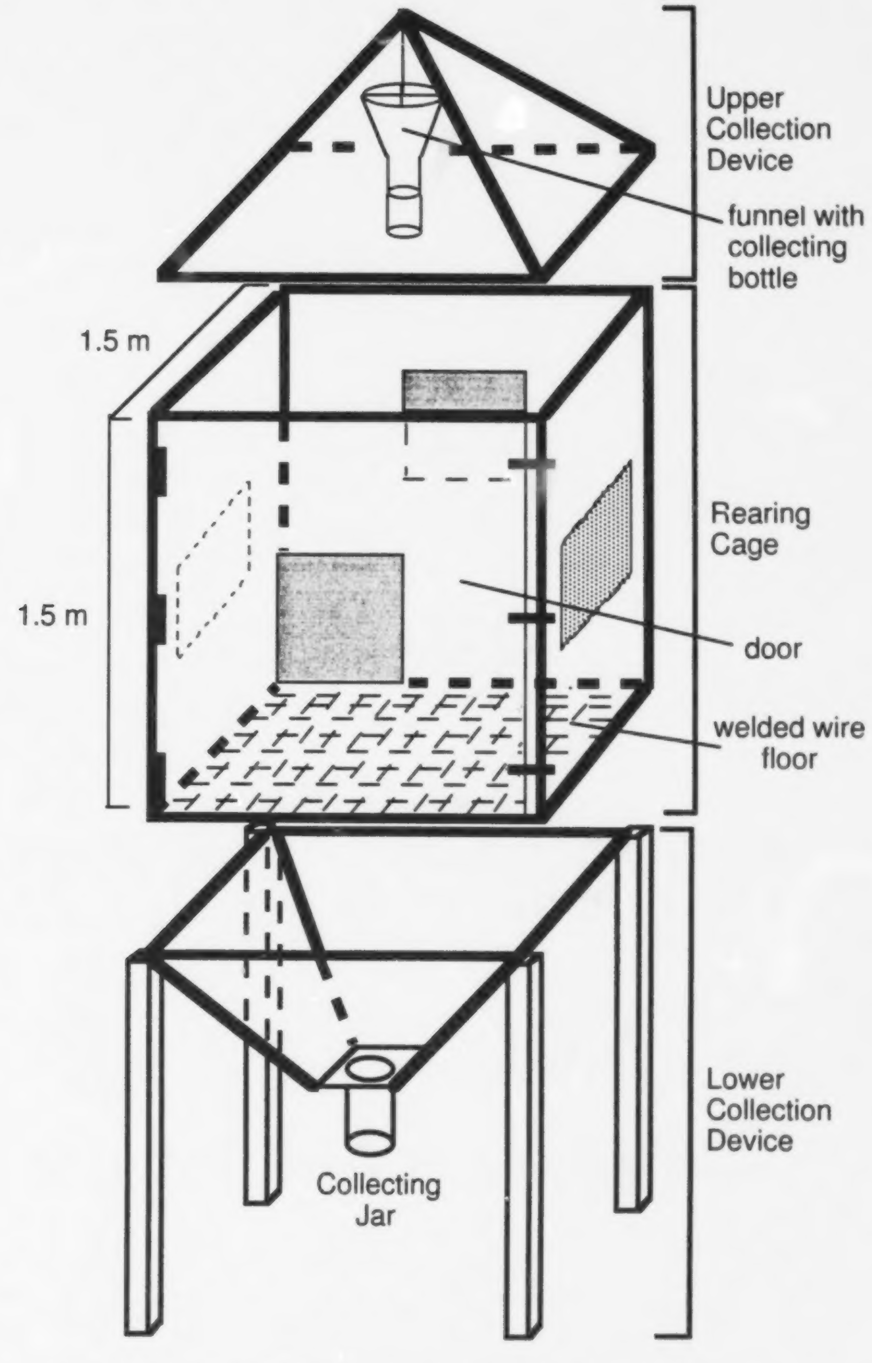
Upper
Collection
Device
funnel with
collecting
bottle
1.5 m
1.5 m
Rearing
Cage
door
welded wire
floor
Lower
Collection
Device
Collecting
Jar

Figure 2-1. Cage design for rearing of arthropods from coarse woody material.

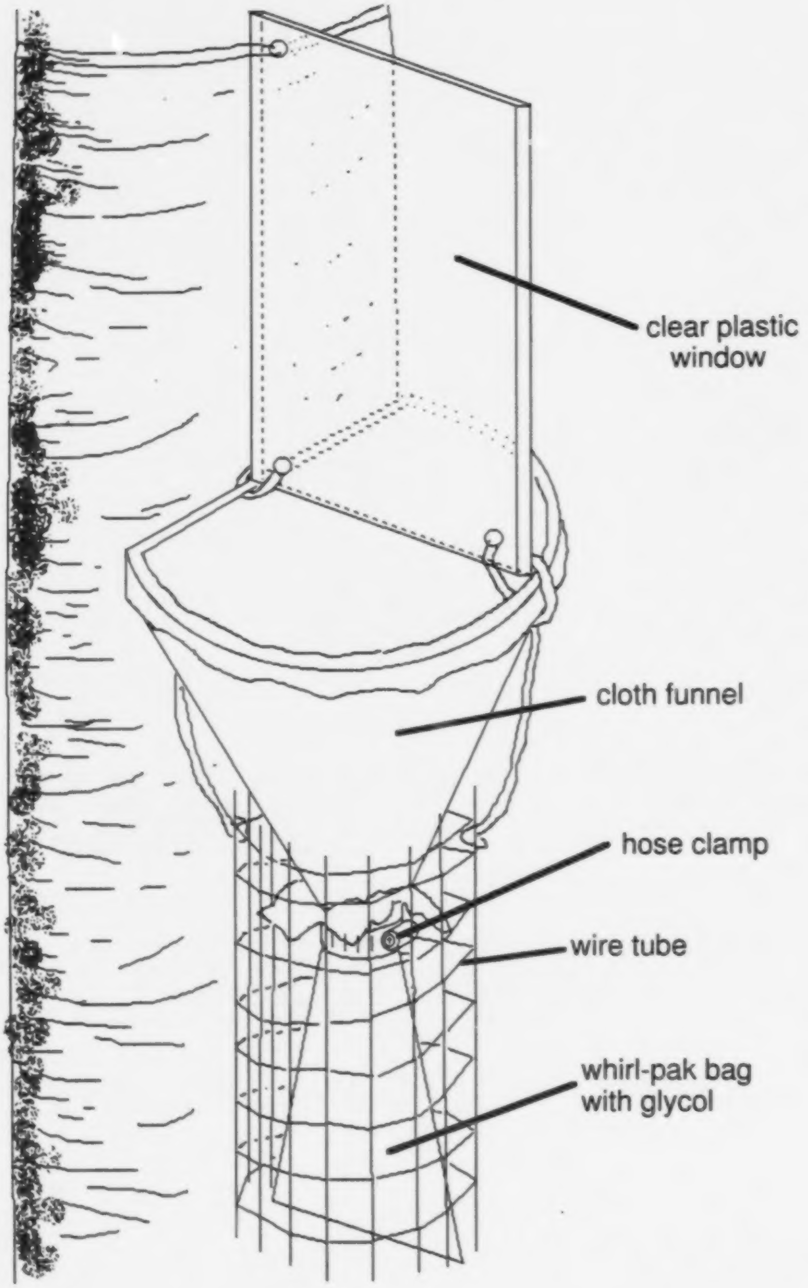
clear plastic window
cloth funnel
hose clamp
wire tube
whirl-pak bag with glycol

Figure 2-2. Window-trap design (modified from Kaila, 1993) for sampling arthropods associated with coarse woody material.

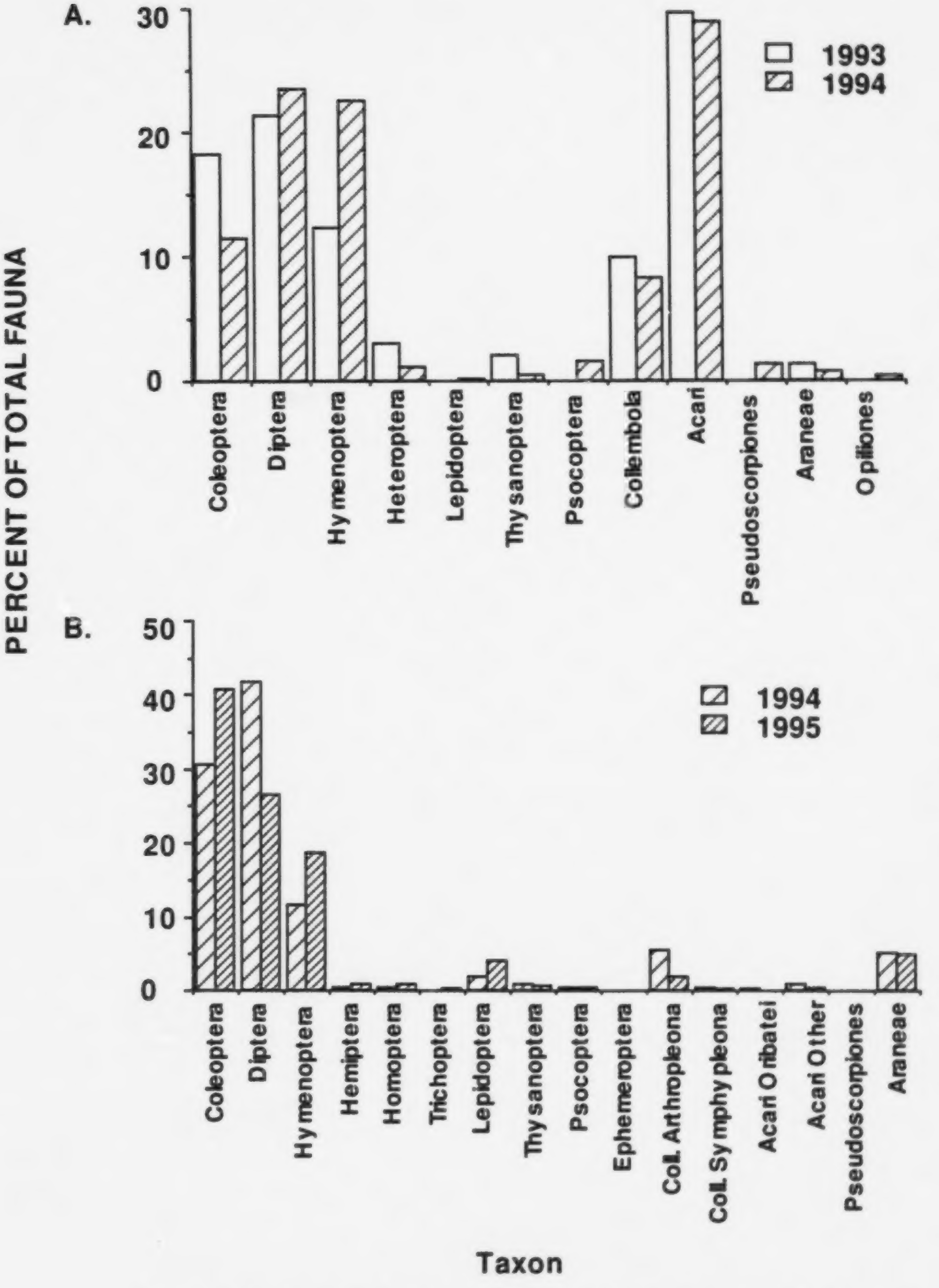

Figure 2-3. The relative abundance of arthropod groups collected from *Populus* coarse woody material, using A. insect rearings from wood bolts, and B. window-traps attached to the boles of snags.

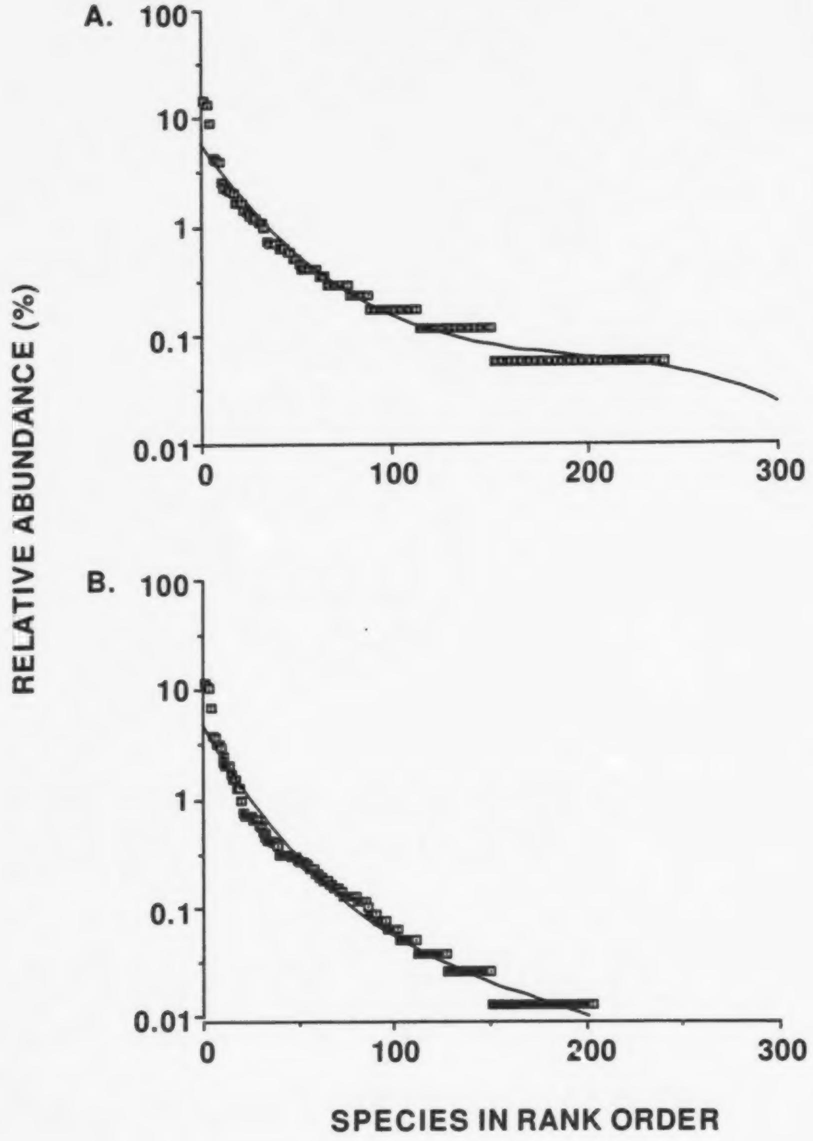

Figure 2-4. Whittaker plots of total saproxylic beetle species abundance collected by A. insect rearings from wood bolts, and B. window-traps attached to the boles of snags.

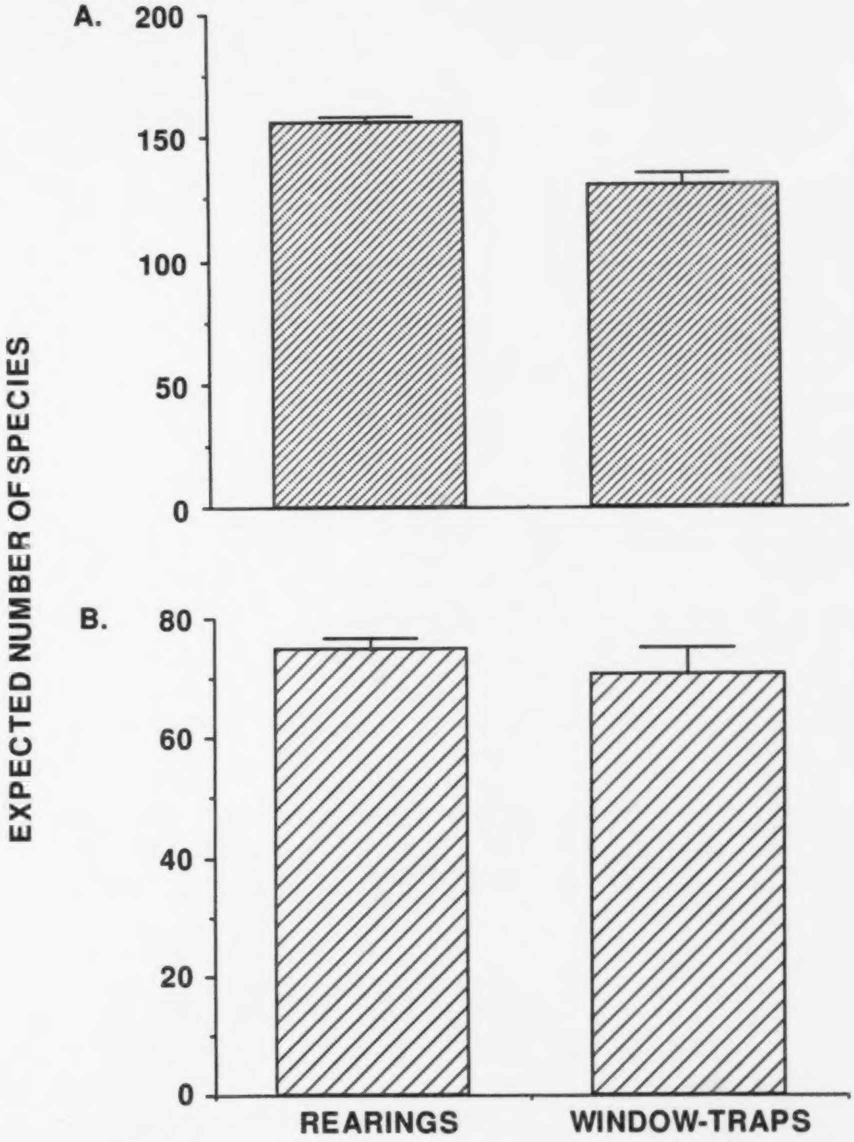

Figure 2-5. Rarefaction (mean±standard deviation) estimates of saproxylic beetle species richness from *Populus* CWM collected by rearings and window-traps;

A. based on a subsample of 1600 individuals from the total catch from rearings (1993 and 1994) and window-traps (1994 and 1995);

B. based on a subsample of 350 individuals from each method in 1994.

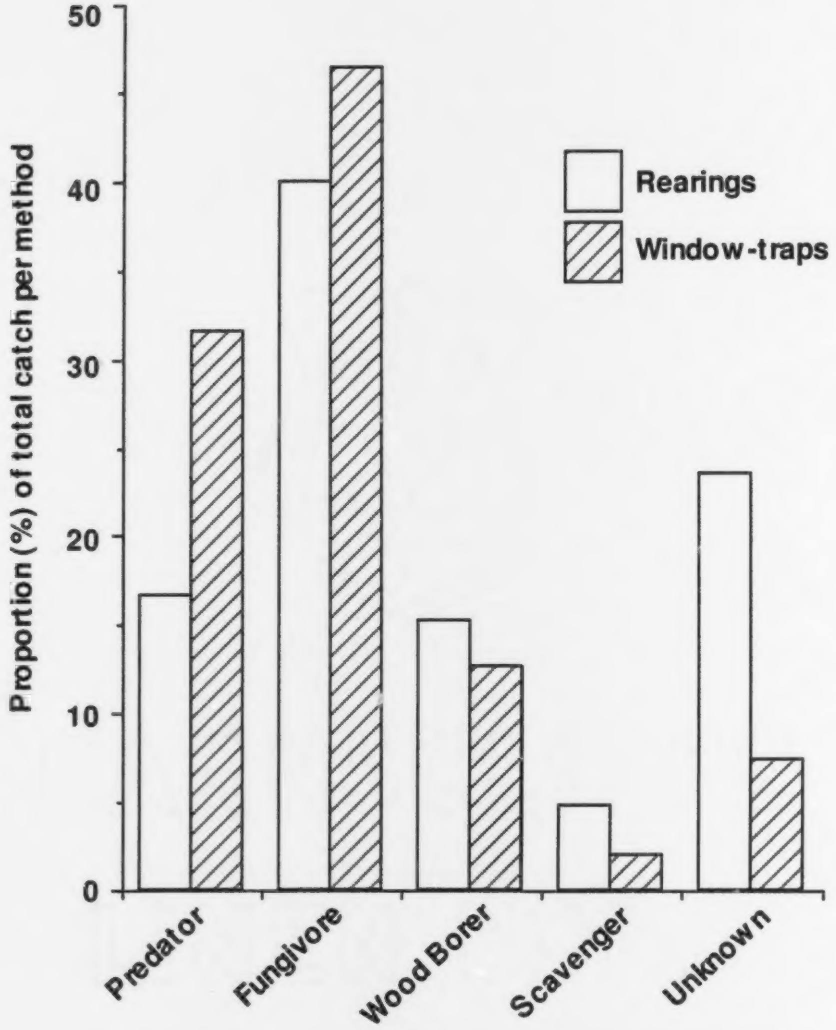

Figure 2-6. The proportion of the total catch of saproxylic beetles partitioned by trophic role. Specimens were collected by rearings from *Populus* logs and snags and window-traps attached to the boles of snags in boreal-mixedwood forests in Alberta, 1993-95.

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3. Spatial and Temporal Variation in the Coleoptera Assemblage Associated with *Populus* Coarse Woody Material

3.1 Synopsis

The Coleoptera fauna inhabiting *Populus* coarse woody material was studied at two sites in northern Alberta over the snow-free months of 1993 through 1995. Beetles were sampled using a combination of insect rearings from bolts cut from snags and logs, and modified window-traps placed on the boles of snags in the forest. In total, 257 beetle species were collected with the composition of assemblages varying significantly between regions, stand age classes, decay classes and years. Species richness and abundance was similar between Lac la Biche and Eureka River, but the fauna was only 42-64% similar with respect to species composition. In general, faunal richness at several taxonomic levels tended to be higher in old forest stands than in mature stands of harvestable age. Stand age also influenced trophic composition, with a significantly higher proportion of predators in old stands and higher fungivore abundance in mature stands. A total of 54 species were unique to old stands and another 44 to mature stands, with the similarity in the fauna across stand ages ranging between 46-68% similar. Although species diversity was similar in wood differing in decay, 29, 32 and 32 species were unique to wood of minimal, moderate, and advanced decay, respectively. In addition, standardized abundance of beetles was similar between snags and logs, however, 46 species were unique to snags and 47 were unique to logs. Detrended correspondence analysis of rearing and window-trap data indicated that factors associated with decay class, region and stand age influenced species distribution across the landscape. Implications of these findings for forest management are also discussed.

3.2 Background and objectives

Approximately 25% of the Canadian boreal forest is a mixture of deciduous and coniferous tree species known collectively as the boreal mixedwood (Peterson and Peterson, 1992; Stelfox, 1995). Trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), and white spruce (*Picea glauca* [Moench] Voss) are the dominant tree species, but white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Miller) B.S.P.), tamarack (*Larix laricina* (Du Roi) K. Koch) and balsam fir (*Abies balsamea* [L.] Miller) are also common (Stelfox, 1995; Peterson and Peterson, 1992; Scudder, 1979). Site conditions such as soil type, elevation, topography and precipitation influence the distribution and abundance of dominant tree species (Oliver, 1992; Stelfox, 1995).

In addition to regulation by site factors, natural forest dynamics in this region have been dominated by periodic wild fires. Fires that leave small islands of unburned forest contribute to the complexity of forest structure, allowing for a diversity of organisms specialized to colonize regions after burns and for mixtures of tree species on similar sites (Ås, 1993). Forest fires, self-thinning in immature stands, blow down of trees, and the impacts of insect pests and diseases, also create a large volume of dead and dying trees (Harmon et al., 1986). This coarse woody material (CWM) consists mainly of snags (standing dead and dying trees), logs (fallen dead trees), stumps, and any root systems that remain, and provides a habitat for a rich community of organisms dominated numerically by arthropods (Danks, 1979).

Arthropod communities associated with CWM are diverse, not only in species, but also with respect to the roles that they play in forest ecosystems (Graham, 1925; Savely, 1939; Howden and Vogt, 1951; Wallace, 1953; Fager, 1968, Speight, 1989). Saproxylic invertebrates are species dependent, during some part of their lifecycle, upon the dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi, or upon the presence of other saproxylics (Speight, 1989). However, other arthropod groups also use dead wood indirectly as shelter or overwintering sites and may not depend directly on dead wood to survive (see Chapter 2). Saproxylic organisms are responsible for the mechanical breakdown of woody material directly, by tunneling and feeding in snags and logs, and through the vectoring of symbiotic fungal species that humify the wood (Speight, 1989).

Saproxylic species are sensitive to man-made disturbance associated with habitat loss such as forest harvesting, and reforestation with native and non-native coniferous tree species on sites previously occupied by deciduous or mixed forest types (Heliövaara and Väisänen, 1984; Speight, 1989; Mikkola, 1991; Warren and Key, 1991; Wilson, 1992). Many saproxylic species are endangered or extinct in parts of northern Europe where intensive forest management has been ongoing for centuries (Heliövaara and Väisänen, 1984; Väisänen et al., 1993; Haila et al., 1994; Käila et al., 1994; Siitonen and Martikainen, 1994).

The first concerted harvest of the aspen-mixedwood in Alberta has begun, with harvesting to follow a 50-70 year rotation, depending on site (Stelfox, 1995). Over time, this management scheme will truncate forest age structure resulting in a reduction of old-growth, here defined as stands older than rotation age. Such changes may affect overall ecosystem integrity, at least partially through loss of species contributing to decomposition, whose populations are concentrated in old-growth forests.

In 1993, I began a study of the Coleoptera associated with *Populus* CWM in aspen-mixedwood forests in north-central Alberta. The objectives of this study were to assess spatial variation in the saproxylic beetle community with respect to geographic region, stand age, degree of decay of CWM, and type of CWM (i.e. snags or logs). An assessment of temporal variation in community structure was also possible since the study took place over three years. In addition, ordination analysis was used to investigate the factors underlying distribution of saproxylic beetle assemblages across the landscape. These data can be used to gain a more general understanding of how forestry practices affect the fauna of CWM.

3.3 Materials and methods

3.3.1 Study sites

Coleoptera communities from *Populus* CWM were sampled at two study sites; one near Touchwood Lake east of Lac la Biche (54° 51' N, 111° 27' W), and the second north of Fairview, near Eureka River (56° 35' N, 118° 37' W), Alberta. Both sites are dominated (>80% of canopy and understory trees) by trembling aspen, and include a mixture of balsam poplar, white spruce and birch in lesser amounts (see Chapter 2). Two stand ages were sampled at each site, mature stands (40-80 years) and old stands (>100 years). Old stands were characterized by relatively large trees (29-42 cm diameter at breast height, DBH), a canopy that was 20-27 m above the ground containing many gaps, and CWM that ranged from 30-

48 cm DBH. Mature forest stands were characterized by smaller trees (15-20 cm DBH), a closed canopy approximately 18-20 m above the ground, and CWM ranging from 8.5-20 cm DBH. In addition, three wood decay stages were used to separate the wood into 'minimally' decayed (decay class 1), 'moderately' decayed (decay class 2), and advanced decayed (decay class 3) wood (see Table 3-1 for decay class criteria). Because CWM of *Populus tremuloides* and *P. balsamifera* are often difficult to identify, especially snags and logs of large diameter and in states of advanced decay, the data could not be reliably partitioned by tree species.

3.3.2 Data collection

Two methods were used to sample beetles from CWM, rearing of insects from wood samples in cages and passive trapping using modified window-traps attached to the boles of snags (Kāila, 1993; see Chapter 2 for details of apparatus and methods). Insect rearings are highly specific, collecting only arthropods within the wood at time of collection, but are time and resource limited. In contrast, window-traps are more wide-sweeping but less selective, and depend mainly on flight activity. Window-trap sampling is also easier to replicate, thus their use provides larger sample sizes.

Wood samples for rearing were cut from snags and logs in late April and early May of 1993, and again from the same stands in April and May 1994. One *Populus* snag and one log were sampled from each of the three decay classes in one old and one mature stand at Lac la Biche and at Eureka River. Bolts 1.2 m in length, from the base, center, and top of each snag or log were returned to the lab sealed in plastic bags and the three bolts from each snag or log were placed in the same rearing cage (see Chapter 2). All rearings were conducted outdoors at ambient temperature and light. The wood samples were held in rearing cages for one year. All emerging arthropods were collected weekly from 16 April-30 August, then biweekly from 30 August-30 September, and preserved in 95% ethanol.

On completion of rearing, the volume of each wood bolt was estimated by measuring its diameter at the midpoint of its length and calculating the volume of a cylinder 1.2 m in length. The volume of the three wood bolts from each snag or log were then summed to give an average volume for each snag or log.

Eighteen window-traps were deployed in each of two old and two mature stands at each region. Two window-traps, one with the top of the window at breast height (ca. 1.3 m) and the second with the top of the window at ca. 2.0 m, were placed on three snags representing each of the three decay classes in each stand. The orientation (i.e. cardinal direction) of both traps on each snag were the same, but was determined randomly by dice roll. Where possible the same snags were sampled in both 1994 and 1995. If snags blew down, another of similar diameter and decay class was chosen as close as possible to the previously sampled snag. Insects were collected biweekly from 18 May-7 October, 1994; and 2 May-28 August, 1995.

3.3.3 Data analyses

Only saproxylic beetles associated with *Populus* CWM were included in analysis, and include all species from Table 3-2. A saproxylic species is hereby defined as one which directly uses CWM and/or its associated biota during some part of its life cycle for reproduction and/or food. This includes predators, scavengers, fungivores, xylophages and phloeophages.

Because volume of CWM reared and the number of days rearing was not the same for all samples, data from rearings were standardized to 0.1 m^3 of wood and 1000 trap-days. Catches from window-traps were standardized to 1000 trap-days to account for differences in sampling effort.

The mean number of taxa collected and their mean standardized abundance from rearing and window-trap samples were analyzed using an analysis of variance (ANOVA, proc GLM) in SAS (Steel and Torrie, 1980). Rearing data was analyzed using a 5-way ANOVA in a split-plot design, with the main effects of region, stand age, decay class, sample type (i.e. snag or log), and year of collection. Window-trap data was analyzed using a 4-way ANOVA in a split plot design, with the main effects of region, stand age, decay class, and year. Parametric analysis was also used to compare trophic structure of beetle assemblages from CWM. Beetle taxa were assigned to one of four trophic roles, predator, fungivore, wood borer, and scavenger, based on the known habits of the predominant life stage found in dead wood. All xylophagous, phloeophagous and ambrosia beetles were included in the wood borer category. Taxa for which trophic role was not known or uncertain were classified as unknown. Mean standardized abundance and proportional abundance represented by each trophic role was compared and tested using GLM in SAS, similar to the models stated above. Full ANOVA tables are presented in Appendices 1-6.

In addition to comparing mean number of taxa, species diversity was measured three ways to minimize the effect of bias of a single method (Grassle et al, 1979; Krebs, 1989). First, to correct for sampling errors and for uneven catches, I calculated an unbiased estimate of species richness using rarefaction (Sanders, 1968; Hurlbert, 1971). Rarefaction predicts the number of species in a subsample taken from the original sample based on probabilities calculated from observed species abundance. Thus, rarefaction is a measure of diversity that can be compared across samples standardized for total capture. A second diversity measure originating from information theory, the Shannon-Wiener index (H'), is based on the assumptions that individuals are randomly sampled from an infinitely large population, and that all species are represented in the sample (Pielou, 1975; Magurran, 1988). The benefits of this method are the ease of computation and its wide use in the literature, which facilitates comparisons with other communities (Magurran, 1988). Thirdly, the Berger-Parker index (d') is a dominance measure, simply the inverse of the abundance of the most dominant species in a sample divided by the total abundance in the sample (Magurran, 1988). In general, the higher the d' the lower the ratio of the most abundant species to the total, and the more even the distribution. A FORTRAN program, similar to that of Krebs (1989) but modified to run on the VAX system at the Northern Forestry Center (Canadian Forest Service) was used to calculate rarefactions. The program StatEcol (Ludwig and Reynolds, 1988) was used to calculate the Shannon-Wiener index, and the Berger-Parker index was calculated directly from spreadsheets using the Excel software package.

I used cluster analysis of Bray-Curtis percent similarity measures with group averaging as the weighting procedure in the program StatEcol

(Ludwig and Reynolds, 1988), to compare relationships of beetle assemblages among different samples and sites.

To better understand factors influencing each species abundance pattern, the standardized abundance of taxa in each sample matrix was subjected to ordination using detrended correspondence analysis (DCA) (Hill, 1973; Hill and Gauch, 1980; Gauch, 1982; ter Braak, 1987) using the computer program CANOCO (ter Braak, 1987). Detrended correspondence analysis is an indirect gradient technique which constructs axes that maximize the variation in abundance of each species across samples, and in doing so helps to identify factors that most influence the observed species distributions. Although several ordination methods were tested, such as principal components analysis and correspondence analysis (ter Braak, 1987), DCA was the ordination method that maximized the spread (variation) in the data points, over axes based on more than a few species. Rare species (species with frequencies less than the frequency of the commonest species divided by five) were downweighted to a score of one, to reduce their influence on the ordination. Only q-matrix (ordination based on the sample unit matrix), providing sample unit ordinations for each trapping method are presented.

Data collected using window-traps were analyzed separately from those collected by rearings. Initially, DCA was conducted only on the saproxylic taxa listed in Table 3-2. However, a broader definition of the community may also include those taxa which facultatively use CWM for overwintering or shelter. For example, many non-saproxylic beetles were reared from *Populus* CWM, including herbivorous and aquatic taxa (Chapter 2). Thus, all 203 taxa collected by rearings (Table 2-2) were also subjected to DCA. No DCA was run for window-trap data using a broader definition of the community associated with CWM because of the difficulty in defining criteria for inclusion of additional species.

3.4 Results

A total of 10,833 beetles were collected by rearings and window-traps between 1993 and 1995, representing over 370 beetle taxa (see Table 2-2 in Chapter 2 for a complete list). However, saproxylic beetles were subjected to further analysis. The distribution and abundance of the 257 saproxylic species is summarized in Table 3-2. Of these, 53 species and two families were collected only by rearings, 96 species and 10 families were collected only by window-traps, and the remaining 108 species and 39 families were collected by both methods.

3.4.1 Regional comparisons

There was no difference in the mean number of taxa collected between regions, with either sampling method (Table 3-3). There was, however, one significant region x decay class interaction for the number of families collected by window-traps (df=2, F=4.93, P=0.0402). More families were collected from decay class 1 snags near Lac la Biche than Eureka River (Figure 3-1A), suggesting that the diversity of families available to colonize new dead wood drops further north.

Rarefaction estimates of species richness from insect rearings shows that Lac la Biche's fauna is more diverse than Eureka River's, for both years (Figure 3-2). Rarefaction estimates for window-traps, however, show the opposite trend for both years (Figure 3-3). The Shannon-Wiener index shows the same regional diversity patterns as the rarefaction estimates; however, the Berger-Parker index indicates that saproxylic beetle diversity is generally higher at Eureka River (Table 3-4).

Overall standardized abundance was also similar between regions (Table 3-3). However, there was a significant region x stand age effect for beetles collected by rearings (df=1, F=15.79, P=0.0032), with greatest standardized abundance in mature stands near Lac la Biche and lowest abundance in old stands near Lac la Biche (Figure 3-4A), suggesting that beetle abundance also differ between regions.

Mean standardized abundance of fungivores collected with window-traps was significantly higher (df=1, F=8.90, P=0.0406) at Lac la Biche than Eureka River (Table 3-5). In addition, there were significant region x age effects for the abundance of fungivores (df=1, F=8.14, P=0.0190), predators (df=1, F=9.03, P=0.0148), and scavengers (df=1, F=9.01, 0.0149), collected in rearings (Figure 3-5A-C). These data suggest that the pattern of fungivore, predator, and scavenger abundance between regions also differs greatly with stand age, with the number of predatory beetles increasing further north.

The proportion of beetles representing each known trophic role is similar among regions for both rearings and window-trap data (Table 3-5), except that the proportion of scavengers collected with window-traps was significantly higher at Eureka River than Lac la Biche (df=1, F=7.01, P=0.0571). The largest proportion of the beetle fauna from CWM at both sites was composed of fungivores, followed by predators (Table 3-5).

Bray-Curtis estimates of saproxylic beetle similarity between regions for 1993, 1994, and both years combined was 54%, 42% and 57%, respectively, based on rearing data; and for 1994, 1995 and both years combined was 58%, 62% and 64% based on window-trap data. Low faunal similarities between regions suggests that faunal composition is somewhat different between the two regions. A total of 142 beetle species were shared between both regions, 47 species were unique to Eureka River, and 68 species were collected exclusively at Lac la Biche (Table 3-2).

3.4.2 Age class comparisons

In general, taxon richness is higher in old forest stands. According to rearing data, old forest stands had significantly higher number of species (df=1, F=10.40, P=0.0104), genera (df=1, F=10.17, P=0.0110) and families (df=1, F=12.47, P=0.0064) than mature stands (Table 3-3). However, data from window-traps showed no significant differences in the number of taxa among age classes (Table 3-3). In addition, there were several significant interactions of age x decay class for the mean number of species (df=2, F=4.76, P=0.0434), genera (df=2, F=5.38, P=0.0330), and families (df=2, F=7.81, P=0.0131) for window-trap collections (Figure 3-1B-D), suggesting that the diversity of taxa adapted to exploit increasingly decayed wood is concentrated in old stands.

Rarefaction estimates show little difference in species richness between old and mature stands for rearings (Figure 3-6) and window-traps (Figure 3-7); however, the Shannon-Wiener and Berger-Parker indices showed that diversity was generally higher for old than for mature stands (Table 3-4).

Mean standardized abundance of saproxylic beetles was significantly higher in mature than in old stands (df=1, F=16.26, P=0.0030) for rearings (Table 3-3). In addition, there were significant interactions of age x decay class (df=2, F=5.20, P=0.0316) and age x year (df=2, F=5.38, P=0.0323) for beetle abundance collected by rearings. Mature stands exhibited higher abundance than old stands for decay classes 2 and 3 (Figure 3-4B) and in 1993 (Figure 3-4C). Window-trap data showed no significant effects of age class on standardized abundance (Table 3-3).

In both stand age classes fungivores and predators were the dominant trophic groups (Table 3-5), but age class effects on trophic structure were evident. Mature stands had a higher mean standardized abundance of fungivores (df=1, F=11.35, P=0.0083), and scavengers (df=1, F=8.65, P=0.0165) than old stands, according to rearing data (Table 3-5). There was also a significant age x decay class interaction (df=2, F=5.84, P=0.0236) and age x year interaction (df=2, F=5.60, P=0.0294) for the mean standardized abundance for scavengers reared from CWM. Scavenger abundance was higher in mature stands than old stands for decay classes 2 and 3 (Figure 3-5D) and for 1993 (Figure 3-5E). There were no significant differences in trophic role abundance according to window-traps (Table 3-5).

The proportion of predators was significantly higher in old stands than in mature stands, based on both rearing (df=1, F=8.82, P=0.0157) and window-trap data (df=1, F=14.06, P=0.0200) (Table 3-5). Window-trap samples also indicated that the proportion of fungivores decreased with increasing stand age (df=1, F=13.21, P=0.0221). There were also significant interactions of stand age with decay class (df=2, F=7.52, P=0.0145) and year (df=1, F=12.76, P=0.0233) for wood borers collected with window-traps. Wood borer abundance in decay classes 2 and 3 is higher in old stands than mature stands, and the proportion of wood borers greatly increased in old stands in 1995 (Figure 3-8).

According to Bray-Curtis similarity measures, the saproxylic fauna of mature and old stands are approximately 46%, 49% and 50% similar for 1993, 1994 and both years, respectively for rearings; and for 1994, 1995 and both years combined 68%, 63%, and 67% similar, respectively, for window-traps. A total of 159 species were collected in old and mature stands; 54 were unique to old stands, and 44 unique to mature stands (Table 3-2).

3.4.3 Decay class comparisons

In general, species richness tended to be lower in wood with lowest levels of decay. There were no significant differences across decay classes for mean number of species, genera, and families (Table 3-3). However, rarefaction estimates of species richness from rearings and window-traps indicated that decay class 1 has the lowest species richness (Figures 3-9 and 3-10). The Shannon-Wiener and Berger-Parker indices of rearing and window-trap data also suggested that species diversity is lowest in decay class 1 (Table 3-4).

There were no differences in mean standardized abundance among decay classes (Table 3-3). However, standardized abundance from rearings indicated a significant interaction of decay class with sample type (df=2, F=4.51, P=0.0439), with lower abundance occurring in decay class 1 logs than in similarly decayed snags (Figure 3-4D). These data suggest that the fauna is adapted to find recently dead material while it is still standing.

Scavengers collected with window-traps had a significantly higher mean standardized abundance (df=2, F=5.19, P=0.0358) in decay class 3 wood (Table 3-5).

In rearings, there was a significantly lower proportion of wood borers in decay class 2 wood than in the other decay classes (df=2, F=6.02, P=0.0219) (Table 3-5). In window-trap catches, a significantly greater proportion of predators was associated with decay class 1 wood than with the other decay classes (df=2, F=5.09, P=0.0375) (Table 3-5).

The saproxylic beetle fauna from decay classes 2 and 3 consistently cluster together as more similar, according to Bray-Curtis similarity indices from rearings and window-traps (Figure 3-11). Also, the fauna from different decay classes clusters together at a higher percent similarity based on window-trap data than for rearing data (Figure 3-11). A total of 164 species were shared across all decay classes, but 29, 32, and 32 species were unique to decay classes 1, 2 and 3 respectively, again suggesting that the fauna changes across decay classes.

3.4.4 Snag and log comparisons

There were no significant differences in the mean number of taxa between snags and logs (Table 3-3). However, rarefaction (Figure 3-12) and the Shannon-Wiener and Berger-Parker indices (Table 3-4) suggest that the fauna from logs is more diverse than snags. There was no difference between snags and logs with respect to standardized abundance (Table 3-3).

Trophic structure between snags and logs was similar, except that a significantly higher proportion of wood borers (df=1, F=24.13, P=0.0008) were collected from snags than from logs (Table 3-5). Most of this difference is attributable to *Trypodendron retusum*.

Snags and logs cluster together at 60%, 44% and 59% for 1993, 1994 and both years, respectively, using Bray-Curtis estimates of faunal similarity. A total of 46 beetle species were collected exclusively from snags, 47 species were unique to logs, and 68 were shared between the two sample types.

3.4.5 Temporal variation in the fauna

There were significantly more species (df=1, F=48.83, P=0.0001), genera (df=1, F=56.92, P=0.0001), and families (df=1, F=9.63, P=0.0061) reared in 1993 than 1994 (Table 3-3); however, window-trap data showed no significant temporal variation in taxon richness (Table 3-3).

Rarefaction estimates of species richness from rearing data was only slightly higher for 1994 than for 1993 (Figure 3-13A), but was much higher in 1994 than in 1995 based on window-trap data (Figure 3-13B). In general, Shannon-Wiener and Berger-Parker indices showed no clear temporal patterns (Table 3-4).

The standardized abundance of reared beetles was significantly higher in 1993 than 1994 (df=1, F=42.03, P=0.0001), whereas, there were no temporal differences in abundance for window-trap data (Table 3-3).

Mean standardized abundance was significantly higher for fungivores (df=1, F=27.00, P=0.0001), predators (df=1, F=7.83, P=0.0119), wood borers (df=1, F=4.20, 0.0554), and scavengers (df=1, F=22.95, P=0.0001) collected by rearings in 1993 than in 1994 (Table 3-5). Wood borers collected by window-traps had a higher mean standardized abundance in 1995 than in 1994 (df=1, F=15.40, P=0.0172) (Table 3-5).

Significantly higher proportions of predators (df=1, F=7.48, P=0.0136), and scavengers (df=1, F=16.14, P=0.0008) were reared in 1993 than in 1994 (Table 3-5). However, the proportion of predators was higher in 1994 than 1995 (df=1, F=23.32, P=0.0085), and the proportion of wood borers higher in 1995 than 1994 (df=1, F=13.00, P=0.0266) according to window-trap data (Table 3-5).

Yearly temporal similarity was 21% and 73% for rearing and window-trap data, respectively, based on Bray-Curtis percent similarity measures. A total of 146 species were collected in all three years, but 42, 51 and 18 species were exclusively collected in 1993, 1994, and 1995, respectively.

3.4.6 Community ordinations

Sample unit DCA of beetle groups collected by insect rearings is presented in Figure 3-14 and the diagnostic data are summarized in Table 3-6. The distribution of saproxylic beetle species seems primarily determined by decay class (λ=0.842) for axis 1 and by geographic region for axis 2 (λ=0.439, Figure 3-14A). A third axis, interpreted to be stand age (λ=0.359), is also relatively important in determining beetle distribution (Table 3-6). However, these three axes explained only 27% of the total variation in beetle distribution, suggesting that unstudied factors primarily determine beetle abundance.

Inclusion of all reared species in the ordination resulted in a reduction in the eigenvalues and in the gradient length (=a measure of spread of the data points) associated with all axes, but the cumulative percent variation explained by these axes remained similar (Table 3-6, Figure 3-14B). The interpretation of the axes also changes. The first axis still relates to decay class, but the second axis now relates to stand age, and the third axis relates to sample type (i.e. snag or log) (Table 3-6). Thus, inclusion of all reared species in the ordination reduces the spread of the data points and the predictive power of the ordination. This result gives some confidence that the DCA restricted to saproxylic species does capture some of the relevant factors determining the distribution and abundance of these species.

In the DCA of beetle groups collected by window-traps (Figure 3-15) distribution of saproxylic beetle species seems determined primarily by region (λ=0.364) for axis 1. I was unable to determine factors contributing to the second axis. In general, the eigenvalues, gradient lengths, and the cumulative percent variation explained by this ordination were low compared to those from rearing data (Table 3-6). These data suggest that rearing data give a better estimation of the factors influencing the distribution of saproxylic species.

3.5 Discussion

The saproxylic beetle assemblage associated with *Populus* CWM in mixedwood forests in Alberta is large, diverse, and dynamic. More than 250 species were collected over the three years of this study. This is a conservative estimate of species richness because one subfamily (Aleocharinae) and 21 other beetle genera were not separated to species (Table 3-2). Furthermore, several other species, mainly from the families Cerambycidae, Buprestidae, and Scolytidae, have been collected from *Populus tremuloides* and *P. balsamifera* in Alberta (Ives and Wong, 1988; D. Langor, pers. comm.), but were not collected during this study. With increased sampling effort, more species will certainly be added to this list.

3.5.1 Spatial and temporal variation

3.5.1.1 Regional variation in the CWM fauna

An overview of studies suggests that regional variation in faunal composition of CWM is not unusual. Siitonen and Martikainen (1994) attributed differences between beetle assemblages of *Populus tremula* L. CWM between Finland and Russian Karelia to different management history of forests. In particular, they argued that changes in the abundance, continuity and type of dead aspen, as a result of intensive forest harvesting in Finland, has reduced faunal diversity in Finnish forests. Käila et al. (1994) showed that abundance of fungivorous beetle species varied substantially between regions of Finland and Russian Karelia, and among different polypores that they inhabit. In addition, studies of deciduous and mixed forest in Sweden (Palm, 1951, 1959; Berg et al., 1994; Ås, 1993) suggest that species diversity was similar among sites, but species composition of the sites were different.

Specific beetle assemblages associated with *Populus* CWM differed between the two regions compared in this study. Although there is no regional effect on taxon richness or standardized abundance (Table 3-3) and only small regional differences in diversity (Table 3-4, Figures 3-2 and 3-3), there were considerable differences in species composition between regions. Only 58% of the species collected were shared between regions; 17% were unique to Eureka River and 25% unique to Lac la Biche.

In this study, all stands sampled were of pyrogenic origin and have not been subjected to intensive forest management, therefore management history is likely not an explanation for the differences seen in the fauna. These findings may simply reflect collecting artifacts, and that increased sampling effort would show less uniqueness between regions. However, faunal differences may also reflect regional variation in site characteristics such as the proximity to mountains, temperature, precipitation, snow cover, soil composition, and presence of particular microhabitats (e.g. fungi). For instance, Eureka River is considerably further north and west than Lac la Biche and may have more faunal elements in common with montane and subarctic regions. In fact, four species, including *Xestobium marginicolle* (LeC.), *Rhyncholus knowltoni* (Thatcher), *Mycetoporus brunneus* Marsh., and *Philonthus crestonensis* Hatch, show a north-western distribution (Bousquet, 1991), and were collected entirely at Eureka River. Nine species from Lac la Biche, including *Dyschirius interior* Fall, *Bellamira scalaris* (Say), *Athous productus* (Randall), *Pyractomena borealis* (Randall), *Mycetophagus pluripunctatus* LeConte, *Pelecotoma flavipes* Melsh., *Elonium diffusum* (Fauvel), and *Mycetochara fraterna* (Say), have primarily central and eastern Canadian distributions (Bousquet, 1991). These findings suggest that in Alberta there is a transition or mixing of the fauna between the lowland regions of central Canada and more upland sites closer to the Rocky Mountains.

3.5.1.2 Age class variation and old-growth dependency.

Concerns about the influence of forest age class on biodiversity has centered on the role of old-growth stands in harboring unique biota highly dependent on such stands (Wilson, 1992; Niemelä et al., 1993a,b). From a conservation viewpoint, it seems reasonable to define stands on harvested landscapes as old if their age exceeds that of the projected harvesting, or rotation age (e.g., Spence et al., 1996, 1997). In the mixedwood forests of Alberta, projected rotation ages range from 50-70 years depending on localized site factors (Stelfox, 1995). Thus, the stands described as 'old' in this study qualify as old-growth. If present harvesting plans continue, however, there will be a truncation of forest age structure across the landscape. There will be abundant habitat for mature forest species, but habitat availability for old-growth species will be severely limited.

Stand age has an important influence on species richness, abundance and composition of saproxylic beetles from CWM. The mean number of taxa collected from rearings (Table 3-3) and the Shannon-Wiener and Berger-Parker diversity indices (Table 3-4) suggest that taxon diversity is higher in old stands. However, there was little difference in species diversity among stand ages as determined by rarefaction (Figures 3-6 and 3-7). Overall, 19% of the fauna were restricted to old stands, 16% were exclusive to mature stands, and the remaining 64% were shared between age classes.

Spence et al. (1997) introduced an index of old-growth dependency (OGD). The OGD index for a species is simply the proportion of landscape standardized abundance found in old-growth stands (i.e., mean standardized abundance in old stands/mean standardized abundance in old and mature stands). Only beetles with abundance greater than 0.2% of the total catch were used, to reduce the effects of rare species. The criterion for an old-growth specialist was any species that had an OGD index of 80% or greater (Spence et al., 1997). This value is rather arbitrary, and any increasing index value denotes increasing dependency on old-growth.

A large number of saproxylic beetles from *Populus* were shown to be dependent upon CWM in old-growth forests. From insect rearings, 18 species showed an OGD index greater than 50%, of which eight were fungivores, four were predators, two were scavengers, three were wood borers, and one species of unknown trophic status (Figure 3-16). Using the 80% criterion proposed by Spence et al. (1997), only two species collected by rearings, one species of *Carpelimus* and *Rhizophagus remotus* LeC., would qualify as old-growth dependent. Little information is available about *Carpelimus* other than it is a scavenger (M. Thayer, pers. comm.), however, *R. remotus* is a specialist predator on bark beetles, namely *Trypodendron retusum* (LeC.). It is interesting that *T. retusum* does not show a similar degree of old-growth dependency.

A total of 42 species from window-traps had an OGD index greater than 50%, of which 15 were fungivores, 14 were predators, seven were wood borers, three were scavengers, and three were of unknown trophic role (Figure 3-17). Nine species, represented by four predators, two wood borers, two scavengers and one fungivore met the 80% old-growth dependency criterion.

The dependence of beetles on old-growth stands has been demonstrated for many forest communities. Speight (1989) identified many saproxylic beetle species as sensitive to loss of old-growth deciduous and coniferous habitats. Väisänen et al. (1993) listed 29 beetle species that were collected only in 250 year old Scots pine-Norway spruce forests in Finland. Studies in Alberta dealing with the litter fauna have also shown that there is some dependence on old-growth stands, with eight species of rove beetle and one ground beetle species qualifying as old-growth dependent (Spence et al., 1996, 1997). Physical features associated with stand age such as: tree and snag density (Siitonen, 1994; Stelfox, 1995), canopy gaps (Rebertus et al, 1993; Schowalter, 1994; Lundquist, 1995), tree size (Siitonen and Martikainen, 1994; Chandler, 1991; Väisänen et al., 1993), and changes in other fungi, plant and animal composition during forest succession (Auclair and Goff, 1971; Jonsell and Nordlander, 1995; Stelfox, 1995) have been suggested as factors influencing species composition in old stands.

This study also demonstrated that beetle trophic composition of CWM also changes during stand succession. Chandler (1991) suggests that fungivore abundance should increase in old stands because fungal abundance and CWM volume are positively correlated (Harmon et al., 1986). In fact, it has been shown that the abundance of many fungivorous beetle species, especially those that feed on fungi and slime molds found under bark, increase in old-growth stands (Chandler, 1991; Chandler and Peck, 1992). The lower abundance of fungivores in old stands than in mature stands found in this study (Table 3-5) is thus counter intuitive. Chandler and Peck (1992) suggested that some fungivorous beetles (e.g. Leiodidae) can disperse far distances and recolonize disturbed habitats quickly. If this is the case, more fungivorous beetles may be collected by window-traps in mature stands simply because beetles are dispersing in an attempt to find suitable host fungi. In old stands there may be less dispersal because host fungal material is plentiful.

The higher proportion of predators collected from CWM in old stands compared to mature stands (Table 3-5), however, is not surprising. Chandler (1987) showed that predatory pselaphid beetles reach maximum species richness and abundance in 100-120 year old forest stands, and attributed this finding to the large volume of leaf litter and CWM found in old stands. In addition, it has been shown for many different community types that predators and top predators enter food webs much later in succession (for a review see Huffaker, 1958; Kitching and Beaver, 1990; and Schoenly et al., 1991).

3.5.1.3 Decay class variation in the CWM fauna

The results from this study suggest that the amount of time elapsed since tree death influences beetle assemblages. Although species richness and abundance was similar across decay classes (Table 3-3, Figures 3-9 and 3-10), the specific fauna associated with each decay class differed. Approximately 11%, 12% and 11% of the beetle fauna was unique to decay classes 1, 2 and 3, respectively, and the remaining 66% were shared among decay classes. Therefore, variation in decay class contributes to biological diversity in mixedwood forests.

There have been many studies of the succession of arthropods into CWM (Blackman and Stage, 1918; Blackman, 1924; Savely, 1939; Derkson, 1941; Howden and Vogt, 1951; Wallace, 1953; Fager, 1968). In general, colonization of dead wood can be broken into three phases. The first phase is often dominated by xylophagous beetles, often from the families Scolytidae and Curculionidae, their associated predators, and some fungivores. In phase two, scolytid abundance begins to drop, secondary sapwood- and phloem-feeding species such as buprestids and cerambycids arrive, and there tends to be an increase in fungivorous and predatory species. Phase three is dominated primarily by fungivores and scavengers, which feed on fungi permeating the wood.

The fauna colonizing *Populus* CWM also follows this general pattern (Table 3-2). The first species into new CWM include the wood borers *T. retusum, Procryphalus mucronatus* (LeC.), and *Hylecoetus lugubris* Say; their predators, *R. remotus*, various species of *Philonthus*, and *Carphacis nepigonensis* (Bern.); and fungivores such as *Epuraea* and *Allandrus populi* Pierce. However, most secondary sapwood feeders showed little dependence on specific decay stages. Many fungivores such as lathridiids, cryptophagids, and *Dolichocis manitoba* Dury and scavengers like *Trogoderma sinistrum* Fall were collected in heavily decayed wood. However, some wood boring taxa such as *Rhyncholus,* and *Tricorynus densus* (Fall), and associated predators, *Teretrius montanus* Horn and *Stenus* spp. are present in later decay stages.

The high abundance and proportion of wood borers associated with decay class 1 (Table 3-5) was expected since this wood is presumably still giving off volatiles, such as phenolics and ethanols, which are attractive to wood borers (Chapman, 1963; Schowalter, 1985). Many wood boring species such as scolytids, cerambycids and buprestids require freshly killed trees due to the higher nutrient value of the wood, or the ability to cultivate fungi in the wood (Abrahamson, 1967; Brewer et al., 1989). However, the relatively high abundance of wood borers associated with decay class 3 was unexpected (Table 3-5). It may be that the fungi associated with decay class 3 wood give off volatiles that are also attractive to many wood boring species (Witcosky et al., 1987). These beetles may have to 'taste' the wood to judge whether it is suitable to breed in, and in doing so, may be collected irregardless of whether they will actually breed there.

Sample unit ordinations for rearing data confirmed that decay class is a major influence on the distribution of beetles (Figure 3-14). Decay influences the physical and biotic characteristics of individual snags and logs through changes in wood moisture and temperature (Hammond, unpublished data; Setälä and Marshall, 1994; Setälä et al., 1995), nutrient levels within the wood (Haack and Slansky, 1987; Schowalter et al., 1992), and the particular species of fungi present at each stage in the decomposition process. Many fungivorous groups such as the Leiodidae, Staphylinidae and Ciidae have special host fungus requirements and are attracted to highly decayed wood (Lawrence, 1973; Wheeler and Blackwell, 1984). Predatory groups are usually generalists and found across all decay types (e.g., *Calasoma frigidum* Kirby, *Platynus decentis* (Say), and *Calathus ingratus* Dejean) but such genera as *Rhizophagus* and *Rhinosimus* feed primarily on scolytid larvae and are often collected from decay class 1 wood.

3.5.1.4 Snags vs. logs

The position of CWM (standing vs. fallen) also influences faunal composition. Although saproxylic beetle abundance was similar between snags and logs, rarefaction estimates of species richness were slightly higher for logs than for snags (Table 3-3; Figure 3-12). Approximately 29% of the fauna was unique to either snags or logs, with the remaining 42% in both sample types. These data are similar to a related study of the beetle fauna of dead pines and spruces in Finland, which showed that a large number of beetles were selective for logs rather than snags (Väisänen et al., 1993).

A higher abundance and proportion of wood borers, primarily the scolytid *T. retusum* , attacking snags than logs (Table 3-5; Figure 3-4D), is likely related to the way in which wood borers select trees. For instance, many bark beetles are initially attracted to large, dark vertical silhouettes (Amman and Cole, 1983; Raffa and Berryman, 1980), as well as to volatiles emanating from suitable host material given off from new dead wood.

Species dispersal abilities may also influence the type of CWM colonized. Beetles such as *Philonthus* spp., *Rhizophagus bruneus* Horn, *Zilora hispida* LeC. and the families Scolytidae, Cerambycidae and Buprestidae, which were collected primarily from snags, may disperse mainly by flight (Table 3-2). Logs, which have a large proportion of their surface area in contact with the ground, may be more readily colonized by species that disperse by walking, such as carabids.

3.5.1.5 Temporal variation in the CWM fauna

Species diversity and standardized abundance fluctuated annually, depending on collection method. The rearings showed substantial differences in both diversity and abundance across 1993 and 1994, at every spatial scale and across many of the trophic levels (Tables 3-3 and 3-5) whereas, window-traps showed some differences in diversity, but little difference in abundance and trophic structure, with only the proportion of predators changing across years (Tables 3-3 and 3-5). Species composition also differed between years with 15% of the fauna unique to 1993, 19% unique to 1994 and 17% unique to 1995. The remaining 60% of the fauna was collected in more than one year.

Several factors influence the distribution and abundance of arthropods temporally. Subcortical temperatures at night and on cloudy days tend to approach air temperature, but direct sunlight greatly increases the temperature under bark, sometimes to lethal limits (Graham, 1925; Savely, 1939). Moderate increases in subcortical temperatures, however, have been shown to speed up development time in beetles, and increase arthropod activity under bark (Savely, 1939; Fager, 1968). Although direct sunlight can increase the temperature of CWM in the winter, sometimes enough to stimulate microarthropod activity (Graham, 1925; Savely, 1939), CWM does not provide enough insulation to stave off freezing. Therefore, arthropods with two year lifecycles have to be heat- and cold-hardy, whereas those strictly using CWM to overwinter must be adapted to freezing.

Precipitation may influence the relative humidity under bark, which has been shown to affect the CWM fauna. Often the relative humidity under bark fluctuates between 50-100%, and this is influenced by the amount of wood decay (Savely, 1939). Many soft-bodied insects, such as beetle larvae, collembola and mites, live under bark to prevent desiccation (Graham, 1925, Savely, 1939; Wallace, 1953; Fager, 1968).

Third, insect populations frequently fluctuate in local abundance. For example, several pest species show population cycles that range anywhere from, 6-16 years for forest tent caterpillar (*Malacosoma disstria* Hubner), 50 years for spruce beetle (*Dendroctonus rufipennis* (Kirby) and 10 years for the Douglas-fir tussock moth (Huffaker et al., 1984; Parry, 1995). The Rothamsted insect survey, which has been monitoring various insect populations since the mid-1800's, has clearly shown that species abundance shows cyclical patterns, and hence diversity in any given year can change dramatically (Taylor, 1986). All these data suggest that to get a good representation of species diversity from a community requires replication of study designs across several years to account for environmental differences across years and changes in individual species abundance.

3.5.2 Ordination analyses

The goals of ordination analyses were to: 1) detect patterns underlying the distribution of saproxylic species by maximizing the variation in the fauna across sample units, 2) see how these patterns might be affected by collection method, and 3) determine what influence facultative saproxylic species have on the interpretation of these axes. Decay class had the most influence on the distribution of beetles collected in rearings, followed by factors associated with region and stand age (Figure 3-14; see above discussion). However, no clear distribution patterns were detected for beetles collected with window-traps (Figure 3-15). Window-traps collect specimens that are not associated with the particular snag sampled, and thus do not adequately reflect faunal variation. This homogenization of samples thus results in poor ordinations. Rearings better sample natural faunal variation among wood bolts resulting in stronger ordinations. Therefore, interpretations of faunal distribution change significantly depending on collection method (Siitonen, 1994; see Chapter 2).

Interpretation of rearing ordinations also changes depending on which beetle species were included in the analysis. A broader definition of community, that included beetle species overwintering or using CWM as shelter, tended to create 'noise' in the ordination and obscured the patterns seen when analysis specifically targeted the saproxylic fauna (Figure 3-14B). Many facultative saproxylic species, primarily chrysomelids and some curculionids (Table 2-2), were collected in snags and logs equally at both regions, but tended to show stand age differences in distribution and abundance. Including these species tends to give an overview of the entire fauna, but obscures the interpretation of the factors influencing saproxylic species.

3.5.3 Implications for insect conservation and forest management

Boreal mixedwood forests in Alberta have undergone little development. Small pockets of white spruce have been harvested, but large scale aspen forestry is relatively new in Alberta. Current thinking on management of boreal forests suggests that forest harvesting should follow a model that approximates, as closely as possible, the effects of natural disturbances such as forest fires (Hansen et al., 1991; Probst and Crow, 1991; Hunter, 1993; Haila et al., 1994; Stelfox, 1995). This model assumes that animal and plant communities in the boreal forest have been adapted to frequent, large scale disturbance, and that emulation of these patterns across the landscape will best conserve viable populations of organisms.

Certain communities, such as the saproxylic fauna, have been shown to be very sensitive to forest management (Speight, 1989; Wilson, 1992; Väisänen et al., 1993). Many of these communities are poorly known and critical to proper ecosystem function. Baseline studies such as this are crucial to understanding community structure and its natural variation in space and time. Based on this understanding, consideration of the following points should help conserve saproxylic insect communities in mixedwood forests:

1). The beetle community in *Populus* CWM is not homogeneous throughout the boreal mixedwood. Although community trophic structure is similar between regions, species composition differed considerably. Complex interactions between spatial scales for taxon richness, standardized abundance, and trophic structure, argues for conservation measures that incorporate all spatial scales. A mixture of large and small reserves, suitably connected and which account for as much variation in habitat structure as possible may be the best method for conserving saproxylic faunas.

2). Truncation of forest age structure, by forest development, may have serious consequences for the fauna dependent on CWM in old-growth stands. Some species associated with CWM show a strong dependence on old-growth stands. In addition, trophic level structure appears to be significantly different between mature and old-growth stands. Experiments have shown that declining diversity in ecosystems alters performance, especially in such processes as community respiration, decomposition, nutrient retention, productivity and vegetation structure (Naeem et al, 1994). Interactions between individuals in different trophic levels are also altered in disturbed habitats (Niemelä et al., 1988; Kitching and Beaver, 1990). In managed forests, maintaining a mosaic of different aged stands across the landscape, similar to a landscape shaped by natural fire dynamics, may act to preserve some of these specialist species. In addition, specific old-growth reserve areas should also be set aside ensuring habitat for old-growth specialists. Increasing the connectivity between forest fragments of different age may also help species that have poor dispersal abilities move between fragments (Ås, 1993).

3). Many beetle species are strongly associated with different types of CWM, with respect to stage of decay and standing or fallen woody material. This further suggests that factors associated with decay class may be important in the distribution of beetles across the landscape. Therefore it is important to maintain forest structure both at the stand level and regional level. Snag and log densities and volumes in aspen-mixedwood stands vary considerably across the landscape (Stelfox, 1995). Maintaining snag and log densities of all decay classes in harvested stands can be achieved by leaving existing snags and logs in cut blocks to act as refugia and sources of new colonization in the developing stand, and by leaving individual and clumps of trees in cut blocks that will later form CWM in later stand succession.

4). It is not enough to choose common species as indicators of community recovery because of seasonal changes in species abundance. In addition, rare species may occupy important roles in the ecosystem, but these require more sampling effort to assess.

Future research goals concerning saproxylic and other insects associated with CWM should focus on several issues. First, more research is required on taxonomy and systematics of these groups (Danks, 1979). Work addressing concerns about invertebrate biodiversity in threatened habitats will become increasingly difficult because the expertise to make reliable species level identification is disappearing (Wilson, 1992). Second, now that the baseline information exists for the fauna associated with *Populus* CWM in Canada, research can focus on how abiotic and biotic factors influence the distribution of these species. Third, research should focus on what effect the coniferous component of the mixedwood has on saproxylic faunas. How much crossover is there in saproxylic faunas from spruce CWM to aspen CWM, and what effect does this have on spatial variation. Fourth, future research should focus on the effects of habitat fragmentation on this fauna, and to determine whether unharvested forest fragments act as reservoirs for old-growth specialists. Studies of the long-term impacts of forest harvesting are required to understand how this fauna reacts to habitat loss. Finally, comparisons of the fauna between harvested and burned areas may shed light on whether the natural disturbance model is appropriate for management sensitive to conservation of biodiversity.

Table 3-1. Criteria used for assigning standing snags or fallen logs to decay classes based on external characteristics.

A. Snags

Decay stage	Leaves	Twigs	% stem coverage by bark	No. of limbs >1 m. long
1	few or absent	many	90-100%	>20
2	absent	few	60-90%	5-19
3	absent	absent	<60%	<5

B. Logs

Decay stage	% stem coverage by bark	% of log covered by mosses or lichens	% of cross-sectional area showing decay
1	90-100%	0-10%	<10
2	60-90%	11-30%	10-50
3	<60%	>30%	>60

Table 3-2. Relative standardized abundance of saproxylic beetle species collected from *Populus* coarse woody material of three decay classes (1-3), in old and mature boreal-mixedwood stands at Eureka River and Lac la Biche, Alberta from 1993-95. Insects were collected by rearing from wood bolts and passive window-traps attached to the boles of snags. Catches from rearings (*) are standardized to 0.1m^3 of wood and 1000 trap days. Catches from window-traps (+) are standardized to 1000 trap days. ([a]P=predator, F=fungivore, WB=wood borer, S=scavenger, ?=unknown; [b]decay class; * or + denotes 1-10 individuals, ** or ++ denotes 11-100 individuals, *** or +++ denotes 101-500 individuals, **** or ++++ denotes >500 individuals)

			Relative Standardized Abundance											
			EUREKA RIVER						LAC LA BICHE					
			MATURE			OLD			MATURE			OLD		
Family	Species	Trophic Role[a]	1[b]	2	3	1	2	3	1	2	3	1	2	3
Aderidae	*Aderus populneus* (Panzer)	?											*	
Anobiidae	*Caenocara scymnoides* LeConte	WB		+		**	+							
	Hemicoelus carinatus (Say)	WB	++	++	+++	* +++	++	** +++	* +++	** ++	++	+++	* ++	** +++
	Ptilinus lobatus Casey	WB	* ++	++	** ++	++	* ++	* ++	+++	++	** +		** ++	** ++
	Tricorynus densus (Fall)	WB	++	+	+++	++	++	++	++	++	++	++	++	+++
	Utobium elegans (Horn)	WB					+	+	+					
	Xestobium marginicolle (LeConte)	WB	++		++		+	+						
Anthicidae	*Anthicus ancilla* (Casey)	S			**									
	Anthicus cervinus LaFte.-Sen.	S		*										
	Anthicus coracinus LeConte	S					*			++				
	Anthicus hastatus Casey	S								**				
Anthribidae	*Allandrus populi* Pierce	F			** +	**								

Bostrichidae	*Endecatomus rugosus* (Randall)	WB										+		+
Buprestidae	*Agrilus liragus* Bart. and Brn.	WB					+	++	+			•		
	Dicerca tenebrica (Kirby)	WB				++	+	•	+			++	++	+
Cantharidae	*Podabrus* spp.	P	+	++	++	++	++	++		+	+	+	+	++
	Silis difficilis LeConte	P		+			+							
Carabidae	*Agonum placidum* (Say)	P					•						•	
	Agonum retractum LeConte	P								+				
	Agonum sordens Kirby	P				+			+		+			• +
	Amara apricaria Paykull	P											•	•
	Amara confusa LeConte	P								••	••			
	Amara cupreolata Putzeys	P											•	
	Amara idahoana (Casey)	P						+						
	Amara lacustris LeConte	P				+							•	
	Amara latior (Kirby)	P										•	+	
	Amara pallipes Kirby	P						•						
	Amara sinuoasa (Casey)	P									•			
	Bembidion spp.	P					+					•	+	
	Bradycellus lecontei Csiki	P										•		
	Bradycellus nigrinus Dejean	P												

			+											
	Calathus ingratus Dejean	P	++	++	++	++	+	++	++	++	++	++	++	++
	Calosoma frigidum Kirby	P	+		+	++	++	++	+++	+++	++	+++	+++	++
	Dyschirius interior Fall	P							+					
	Dyschirius longulus LeConte	P								**				
	Platynus decentis (Say)	P	+++	** +++	+++	+++	+++	+++	++++	** +++	+++	* ++++	* ++++	++++
	Pterostichus adstrictus Escholtz	P								+				+
	Pterostichus pensylvanicus LeConte	P								+				
	Pterostichus punctatisimus (Randall)	P												+
	Stenolophus conjunctus (Say)	P				*				** +	**		*	
	Syntomus americana Dejean	P								+				
	Trichocellus cognatus (Gyllenhal)	P					+				**		*	**
Cephaloidae	*Cephaloon tenuicorne* LeConte	WB		+	++	++	++	++	++	++		++	+	+
Cerambycidae	*Bellamira scalaris* (Say)	WB											+	
	Grammoptera subargentata (Kirby)	WB	++	++	++	* +	+	++	+++	+	++	* ++	++	++
	Hyperplatys aspersa (Say)	WB										*		
	Judolia montivagens (Couper)	WB			+									
	Trachysida mutabilis (Newman)	WB	+	++			+		+++	++	++	* ++	* ++	
Cerylonidae	*Cerylon castaneum* Say	F	++	*** ++	* ++	* ++	** ++	** ++	++	++	** ++	* ++	** +++	* ++

Ciidae	*Cis americanus* Mannerheim	F		**	**			*			**	*	**	
			++	+	++	+		+				+		+
	Cis fuscipes Mellie	F												
						+				+				
	Cis levettei (Casey)	F												
												+		+
	Cis pistorius Casey	F											*	
	Dolichocis manitoba Dury	F									**		*	
			+	++	+	+						++	+	++
	Orthocis punctatus (Mellie)	F												
									+		+			+
	Sulcacis curtula (Casey)	F		***		*	*	*	**	**		*	*	
Clambidae	*Clambus pubescens* Redtenbacher	F												
			+	++	++									
Coccinellidae	*Psyllobora vigintimaculata* (Say)	F								**				*
									++		+		+	
	Scymnus spp.	P												
				+	++		+	++	++		++	++		+
Corylophidae	*Molamba biguttata* LeConte	F	**	**	**	***	**	**	***	***	**	**		*
			++	++	++	++	++	++	+++	++	++	+++	++	++
	Orthoperus scutellaris (LeConte)	F		*		*	*	*		**	*		*	*
				+			++					+		+
Cryptophagidae	*Atomaria (Anchicera) ephippiata* Zimmerman	F		**	**	**	**	**	**	***	**	*		*
			++	++	++			+	++			+		
	Atomaria (Anchicera) spp.	F	**								*			
			++	++	++	+	++	+	++	+		++	++	++
	Atomaria (Atomaria) spp.	F	*			**	**	*		**	*	**	*	*
			+	++	+		++	++	++	++	+	++		+
	Antherophagus ochraceus Melsheimer	F												
				++				++	+	++		++		
	Caenoscelis spp.	F		*										
			++				+		++		++		+	
	Cryptophagus acutangulus Gyllenhal	F											*	*
					+			++		+		+		++
	Cryptophagus laticollis Lucas	F								**				

			++											
	Cryptophagus tuberculosis Maklin	F	++	++	+++	++	+++	+++	++		++	++	++	++
	Henoticus spp.	F	** +	** ++	+	* ++	* ++	++	+	++	**	++	* +	* ++
Cucujidae	*Cucujus clavipes* Fab.	P	++	* ++	* ++	* ++	** ++	++	++	** ++	++	* ++	* ++	** ++
	Dendrophagus cygnaei Mannerheim	P	+						+					
	Laemophloeus biguttatus (Say)	P							+					
	Pediacus fuscus Erichson	P			+		++							
Curculionidae	*Cossonus pacificus* Van Dyke	WB	++	* ++	++	++	+++	+++	++	+	++	+++	++	* ++
	Cryptorhynchus lapathi (L.)	WB	*			*								
	Phloeophagus canadensis Van Dyke	WB		* ++			* ++			**		++	++	++
	Rhyncolus brunneus Mannerheim	WB			***									
	Rhyncolus knowltoni (Thatcher)	WB			**									
Dermestidae	*Dermestes caninus* Germar	S							+					
	Dermestes lardarius L.	S	+					* +			++			
	Trogoderma sinistrum Fall	S			* ++	*	* ++	++	+	**	*	++		* ++
Elateridae	*Ampedus apicatus* (Say)	P		*	++	+	++	* +	+		**		++	++
	Ampedus deletus (LeConte)	S	++	++	++	++	++	++	++	++	++	++	* ++	* ++
	Ampedus luctuosis (LeConte)	S	+	+	++				++					+
	Ampedus mixtus (Herbst)	S			+	++	+	++	+				++	

	Athous productus (Randall)	S										*		
	Ctenicera resplendens (Escholtz)	S		+			++	++	++	++	+	++		++
	Denticollis denticornis (Kirby)	S		**		+		+		**	**		* +	*
	Megapenthes stigmosus (LeConte)	S						+	+					
Endomychidae	*Lycoperdina ferruginea* LeConte	F												+
Erotylidae	*Dacne* (?) *californica* (Horn)	F		+		+				+				
	Triplax (?) *californica* LeConte	F		++	++	+	+++	++	++++	++++	+++	+++	* +++	++
Eucinetidae	*Eucinetus punctulatus* LeConte	F	++	+			++	+	++			++	** ++	++
Eucnemidae	*Dirhagus pectinatus* (LeConte)	?	++	++		+		++		+		+	+	
	Epiphanis cornutus (Escholtz)	?	+		++	**	+	++	+		+	+		+
	Hylis terminalis (LeConte)	?							++		+			
Histeridae	*Abraeus bolteri* LeConte	P					+				+			
	Paramalus bistriatus Erichson	P					+						*	
	Platysoma lecontei Marseul	P				*	++					+		
	Teretrius montanus Horn	P			* ++		++	++	+			++	++	* ++
Hydrophilidae	*Cercyon cinctus* Smetana	S					**	+	+	**	*	*		
	Cercyon pygmaeus (Illiger)	S				+		++			** +			
Lampyridae	*Ellychnia corrusca* (L.)	P								+		+		+
	Pyractomena borealis (Randall)	P										*		

									+			++	++	
Lathridiidae	*Cartodere constricta* (Gyllenhal)	F	*			*	**	**			**	**	*	*
			++	++	+	++			++	++	++		++	
	Corticaria sp A	F	**	**	**	***	**	**	**	***	**	*	**	*
				++	++			++	+	+	++	++	++	++
	Corticaria sp B	F												
			+			++		+	++		++		+	+
	Corticaria sp C	F												
			+		++	+	++	++				++	+	+
	Corticaria sp D	F	*					*		**	**	*	*	**
			+	++	++	++	++	++	++	+	++	+	++	++
	Corticaria sp E	F										*		
			+			++	++	++	+	+	++	+		++
	Corticaria sp F	F											*	
				++										
	Corticarina spp.	F			*									*
	Cortinicara gibbosa (Herbst)	F								**				
							+					+		
	Enicmus sp A	F	**	**	**	**	**	**	**	**	**	*	*	*
				+	++		+					++	+	++
	Enicmus sp B	F									**			
					+									
	Enicmus sp C	F												
				+					++	++	++		+	+
	Lathridius sp A	F	**	**	*	**		**	**	**	*	*	**	*
			++	++	++	++	++	++	++	++	++	++	++	++
	Lathridius sp B	F												*
			+	++	++	+	++	++	++	+	++	+		+
	Melanopthalma pumilla (LeConte)	F	*										**	
			+++	++++	+++	+++	+++	++++	++++	++++	++++	++++	+++	++++
	Melanopthalma villosa (Zimmerman)	F												
			++	++	++	+++	+++	+++	++++	++++	++++	++++	+++	++++
Leiodidae	*Agathidium* spp.	F		*			*	*	*	**	**	*	*	
			+++	++	++	+++	++	+++	+++	++	++	+++	+++	+++
	Anisotoma globososa Hatch	F											*	
			+	+	+		+	++					+	+

	Anisotoma horni Wheeler	F											+	
	Anisotoma spp.	F	++		+			++						
	Anogdus spp.	F	** ++		+					**			*	
	Catops alsiosus (Horn)	S											+	
	Catops americanus Hatch	S	+			+			+					
	Catops basilaris Say	S	+	+	+	+	+							++
	Colon spp.	F	+											
	Hydnobius spp.	F	+											
	Leiodes spp.	F	+											
Lucanidae	*Platycerus piceus* (Kirby)	S			+									
Lycidae	*Dictyopterus thoracicus* (Randall)	P				+								
Lyctidae	*Lyctus planicollis* LeConte	WB	++	++	++	++	++	++	++	++	++	+++	++	+++
Lymexylidae	*Hylecoetus lugubris* Say	WB					+		+	++		+++	* +	++
Melandryidae	*Dircaea liturata* (LeConte)	?		++					++					
	Enchodes sericea (Haldeman)	?		+		+	* ++		++	++	++	* ++	++	+
	Hallomenus scapularis Melsheimer	F						*						
	Melandrya striata Say	?	+++	** ++	* ++	* +++	+++	** ++	+++	** +++	** ++	+++	* +++	++
	Orchesia castanea (Melsheimer)	F							+	++	+	+	*	++
	Phryganophilus collaris LeConte	?												

														◆
	Zilora hispida LeConte	?	◆◆		◆◆	◆	◆◆		◆	•• ◆◆		◆	• ◆◆	◆
Micropeplidae	*Micropeplus laticollis* Maklin	F		◆	◆									
Mycetophagidae	*Mycetophagus distinctus* Hatch	F	◆	••	◆◆	◆	◆◆	•• ◆◆	◆	◆	◆	◆◆	• ◆◆	◆◆
	Mycetophagus pluripunctatus LeConte	F							◆	◆◆	◆	◆◆		
Nitidulidae	*Colopterus truncatus* (Randall)	F		◆			◆	◆						
	Epuraea spp.	F	•• ◆◆◆	◆◆	◆◆	•• ◆◆◆	•• ◆◆	◆◆◆	◆◆◆	◆◆◆	• ◆◆	• ◆◆◆◆	• ◆◆◆	• ◆◆
	Glischrochilus moratus Brown	F	• ◆◆	◆	◆	•• ◆◆		◆◆	◆◆	◆	◆	◆◆	◆	◆◆
	Glischrochilus quadrisignatus (Say)	F					◆				••			
	Glischrochilus sanguinolentus (Olivier)	F	◆			◆◆	• ◆					◆		
	Glischrochilus siepmanni Brown	F	◆◆			◆◆	• ◆◆	◆◆	◆◆	◆◆	•• ◆◆	◆◆◆	◆◆	◆
Pselaphidae	*Actium* spp.	P			◆			◆						
	Batrisodes spp.	P	◆				•		◆		◆	◆◆	• ◆◆	◆
	Euplectus duryi Casey	P		•				◆◆	◆◆			◆◆	•	◆◆
Ptiliidae	*Acrotrichus* spp.	F	◆◆	•• ◆◆	◆◆	•• ◆	•• ◆	•• ◆◆	◆◆	•• ◆	◆◆	• ◆◆	• ◆	•• ◆◆
	Ptiliidae spp.	F	◆◆		• ◆	◆		•	• ◆	◆		•	•• ◆◆	• ◆◆
Pyrochroidae	*Dendroides testaceus* LeConte	F	◆◆	••			◆◆	• ◆◆	◆◆	◆◆	◆◆	◆	◆◆	
	Schizotus cervicalis Newman	F						• ◆	◆		••	•	•	•
Rhipiphoridae	*Pelecotoma flavipes* Melsheimer	?								◆	••		•	•

Rhizophagidae	*Monotoma picipes* Herbst	F				+	+							
	Rhizophagus dimidiatus Mannerheim	P				*	++							
	Rhizophagus bruneus Horn	P	++++	* +++	+++	++++	* +++	++++	+++	**	++	* ++++	+++	+++
	Rhizophagus remotus LeConte	P	** +++	** ++	* +	*** +++	*** ++	** +++	** ++	++	++	** +++	* ++	++
Salpingidae	*Rhinosimus viridiaeneus* Randall	P							+				++	++
	Sphaeriestes virescens (LeConte)	P					*	+						
Scaphidiidae	*Baeocera* spp.	F		**		**	*	*						*
Scolytidae	*Procryphalus mucronatus* (LeConte)	WB	**	* ++		** +	**	*	** +	**		*		*
	Trypodendron retusum (LeConte)	WB	*** +++	++	++	*** +++	++	+++	** ++	++	++	*** +++	* +++	+++
Scraptiidae	*Anaspis rufa* Say	?		++	+									
	Canifa pallipes (Melsheimer)	?	++	** ++	++	** +	** ++	++	++	** +	+	++	++	* ++
Scydmaenidae	*Stenichnus ovipennis* (Casey)	P							+					*
Sphindidae	*Sphindus americanus* LeConte	F								+		+	++	+
Staphylinidae	*Acidota crenata* (Fab.)	P			+			+	+			+		+
	Acidota quadrata (Zetterstedt)	P			+									
	Aleocharinae	?	*** +++	** +++	*** +++	** +++	*** +++	** +++	*** +++	**** +++	*** ++	** +++	** +++	** +++
	Anomognathus spp.	P	**				++					*		
	Anotylus rugosus (Fab.)	S						*			*			
	Anotylus sobrinus (LeConte)	S			**				**	**				*

			+	+				+	+	+			
Atrechus macrocephalus (Nordman)	P											*	
Bledius gravidus Casey	S						*						
Bledius strenuus Casey	S						*						
Bolitobius horni Campbell	P											+	
Bolitopunctus muricatulus (Hatch)	P					+							
Bryophacis smetanai Campbell	P										+		+
Bryoporus rufescens LeConte	P						*		**				
Carpelimus sp A	S	**		*	*					**		*	
Carpelimus sp B	S				**		*						
Carphacis nepigonensis (Bernhauer)	P	+++	* ++	+	* +++	++	* +++	+++	++		* ++++	* +++	+++
Elonium barri Hatch (=*Hapalaraea hamata* (Fau	S		+		+	++	++				+	+	
Elonium diffusum (Fauvel)	S										*		
Eusphalerum fenyesi (Bernhauer)	?							+			+		
Gabrius brevipennis (Horn)	P										+		*
Hapalaraea floralis (Paykull)	P											*	
Heterothops fusculus LeConte	P											+	+
Heterothops pusio LeConte	P											*	
Homalota spp.	P	*			*								

Lathrobium fauveli Duvivier	P		*			+	++		**				
Lathrobium fulvipenne Gravenhorst	P												*
Lordithon bimaculatus (Couper)	P	+		++	++	+++	++				+++	* ++	++
Lordithon fungicola Campbell	P			++	++	++	++	++	+		++	++	++
Lordithon longiceps (LeConte)	P					++			+				
Lordithon thoracicus (Fab.)	P			+	+								
Mycetoporus americanus Erichson	P	+						+					++
Mycetoporus brunneus Marsh.	P					*							
Mycetoporus splendidus (Gravenhorst)	P	+	+				++	+			++	+	
Neohypnus obscurus (Erichson)	P						*			*			*
Nudobius cephalus (Say)	P	**	+		** +	*	* +		+	**	*	++	
Olisthaerus megacephalus (Zetterstedt)	P	++		++	+	++	++				+	* +	*
Ontholestes cingulatus (Gravenhorst)	P								+	++			
Oxyporus occipitalis Fauvel	F	+											
Philonthus concinnis (Gravenhorst)	P							**					
Philonthus crestonensis Hatch	P				+								
Philonthus cyanipennis (Fab.)	P	+				+		++		++	++	++	++
Philonthus occidentalis Horn	P								**				
Philonthus picicornis Horn	P										*		

		+											
Philonthus pugetensis Hatch	P												*
Philonthus varians (Paykull)	P							**					
Philonthus varius Gravenhorst	P											*	
Phloeonomus lapponicus (Zetterstedt)	S	*		*	**	**					*		
Platystethus americanus Erichson	S					+				**			
Proteinus limbatus Maklin	?									+			
Pseudopsis sagitta Herman	P							+				*	++
Quedius caseyi Scheerp.	P				+								
Quedius criddlei (Casey)	P			*		+	*	+			++		++
Quedius fulvicollis (Stephens)	P												*
Quedius plagiatus Mannerheim	P	++	** ++	+	* ++	* ++	* ++	++	++	++	* ++	* ++	* ++
Quedius rusticus Smetana	P		++	++		++	+	+	** +	+	+		
Quedius simulator Smetana	P		+		+				**				
Quedius velox Smetana	P	++	* ++	+	++	++	++	+		+		*	
Sepedophilus littoreus (L.)	F											*	
Sepedophilus testaceus (Fab.)	P				* +							*	
Siagonum punctatum LeConte	S	+	+	+		++			+		+		+
Staphylinus pleuralis LeConte	P			+									

	Stenus dolosus Casey	P			**									
	Stenus immarginatus Maklin	P										+		
	Stenus pinguis (Casey)	P								**				
	Stenus spp.	P			*									
	Tachinus basalis Erichson	P										+		
	Tachinus elongatus Gyllenhal	P	++	++	++		+		++	++	+		+	
	Tachinus frigidus Erichson	F			+	+	+							
	Tachinus fumipennis (Say)	P		+	+	+							+	
	Tachyporus borealis Campbell	P								**		+		
	Tachyporus inornatus Campbell	P								**				
	Tachyporus maculicollis LeConte	P				+								
	Tachyporus mexicanus Sharp	P	+	++	+	*				** ++				
	Tachyporus nimbicola Campbell	P		+										
	Tachyporus nitidulus (Fab.)	P		**			*				**			
	Tachyporus rulomus Blackweld	P					**			**			*	
Tenebrionidae	*Bius estriatus* (LeConte)	F		*	+								+	*
	Mycetochara fraterna (Say)	F							++	++		++	++	+
	Platydema americanum Cast. and Brul.	F				+	+	+				+	*	+
	Scaphidema aeneolum (LeConte)	F	**	**										

					+				+		+			
Trogossitidae	*Upis ceramboides* (L.)	F	++	+	++	++	++	++	++			++	++	++
	Ostoma ferruginea (L.)	P			++	+								+
	Tenebroides mauritanicus Chevrolet	P		*						+		*	+	
	Thymalus marginicollis (L.)	P	++	++	++	*	++	*	++	++	**	+	* ++	++

Table 3-3. Mean (±standard error) number of families, genera, species, and standardized abundance, per sample, of saproxylic beetles collected by rearings and window-traps from snags and logs of three decay classes in old and mature aspen-mixedwood stands near Lac la Biche and Eureka River, Alberta, from 1993-95.

	Eureka River	Lac la Biche	Old stands	Mature stands	Decay class 1	Decay class 2	Decay class 3	Snags	Logs	1993	1994	1995
Rearings												
Number of Families	8.6±0.6	9.1±0.6	10.5±0.6	7.2±0.6	8.0±0.8	10.4±0.8	8.3±0.8	9.6±0.6	8.2±0.6	10.5±0.7	7.3±0.7	-
Number of Genera	12.5±1.3	13.9±1.3	16.2±1.3	10.2±1.3	11.6±1.6	15.2±1.6	12.7±1.6	13.9±1.3	12.5±1.3	17.8±0.8	8.7±0.8	-
Number of Species	12.5±1.3	14.3±1.3	16.5±1.3	10.5±1.3	11.9±1.6	15.8±1.6	12.7±1.6	14.1±1.3	12.7±1.3	17.9±0.9	9.0±0.9	-
Abundance	217.5±23.0	230.0±23.0	158.1±23.0	289.4±23.0	247.2±28.2	251.7±28.2	172.4±28.2	242.0±23.0	205.5±23.0	374.6±32.9	72.9±32.9	-
Window-traps												
Number of Families	12.0±1.7	13.3±1.7	13.5±1.7	11.7±1.7	12.6±0.4	12.8±0.4	12.5±0.4	-	-	-	13.5±0.8	11.7±0.8
Number of Genera	17.2±2.6	18.4±2.6	19.1±2.6	16.5±2.6	17.8±0.8	17.9±0.8	17.7±0.8	-	-	-	19.5±1.3	16.1±1.3
Number of Species	18.8±3.0	20.0±3.0	21.1±3.0	17.7±3.0	19.5±0.9	19.3±0.9	19.4±0.9	-	-	-	21.3±1.5	17.5±1.5
Abundance	346.3±98.0	506.5±98.0	470.3±98.0	382.5±98.0	526.5±53.9	377.5±53.9	375.2±53.9	-	-	-	399.2±37.7	453.6±37.7

Table 3-4. Shannon-Wiener (H') and Berger-Parker (1/d') diversity indices based on saproxylic Coleoptera collected using rearings of *Populus* snags and logs, and window-traps on snags, of three wood decay classes in old and mature boreal-mixedwood forests near Lac la Biche and Eureka River Alberta, 1993-95. Index calculations are based on pooled samples from each sample unit. See text for explanation of indices.

		Insect rearings		**Window- traps**	
Year	**Sample Unit**	**Shannon-Wiener H'**	**Berger-Parker (1/d')**	**Shannon-Wiener H'**	**Berger-Parker (1/d')**
1993	Eureka River	3.21	6.71	-	-
	Lac la Biche	3.28	4.48	-	-
	Old stands	3.37	5.46	-	-
	Mature stands	3.22	4.31	-	-
	Decay class 1	2.47	2.47	-	-
	Decay class 2	3.45	4.46	-	-
	Decay class 3	3.40	4.13	-	-
	Snags	3.10	4.06	-	-
	Logs	3.47	5.98	-	-
1994	Eureka River	3.23	4.92	3.62	5.15
	Lac la Biche	3.65	12.82	3.34	4.73
	Old stands	3.45	6.02	3.65	6.99
	Mature stands	3.58	11.23	3.36	4.83
	Decay class 1	2.80	3.24	3.28	4.46
	Decay class 2	3.46	7.35	3.53	5.61
	Decay class 3	3.24	7.35	3.64	7.81
	Snags	3.40	8.84	-	-
	Logs	3.48	6.28	-	-
1995	Eureka River	-	-	3.60	8.00
	Lac la Biche	-	-	3.42	7.29
	Old stands	-	-	3.57	8.33
	Mature stands	-	-	3.41	5.49
	Decay class 1	-	-	3.39	6.80
	Decay class 2	-	-	3.44	5.40
	Decay class 3	-	-	3.56	6.62
Years Combined	Eureka River	3.36	6.57	3.72	6.32
	Lac la Biche	3.70	5.78	3.46	5.98
	Old stands	3.61	6.80	3.69	7.57
	Mature stands	3.49	5.10	3.47	5.68
	Decay class 1	2.68	2.84	3.42	5.29
	Decay class 2	3.62	5.43	3.61	7.04
	Decay class 3	3.69	5.52	3.71	7.24
	Snags	3.38	4.90	-	-
	Logs	3.68	6.94	-	-

Table 3-5. Mean (±standard error) standardized abundance and proportional abundance of fungivores, predators, wood borers, scavengers and unknown roles, per sample, of saproxylic beetles collected by rearings and window-traps from snags and logs of three decay classes in old and mature aspen-mixedwood stands near Lac la Biche and Eureka River, Alberta, 1993-95.

	Eureka River	Lac la Biche	Old stands	Mature stands	Decay class 1	Decay class 2	Decay class 3	Snags	Logs	1993	1994	1995
Rearings: Abundance												
Fungivores	91.1±12.6	87.4±12.6	59.3±12.6	119.3±12.6	83.5±15.4	113.9±15.4	70.4±15.4	91.1±12.6	87.4±12.6	144.3±14.9	34.2±14.9	-
Predators	40.3±7.9	34.2±7.9	38.2±7.9	36.4±7.9	42.5±9.7	47.2±9.7	21.9±9.7	29.9±7.9	44.5±7.9	54.3±8.6	20.2±8.6	-
Wood Borers	40.9±16.2	27.1±16.2	31.4±16.2	36.5±16.2	70.2±19.8	8.6±19.8	23.0±19.8	51.3±16.2	16.6±16.2	57.8±16.4	10.12±16.4	-
Scavengers	10.3±2.1	11.1±2.1	6.4±2.1	14.9±2.1	7.8±2.5	10.8±2.5	13.5±2.5	9.7±2.1	11.6±2.1	19.7±2.7	1.7±2.6	-
Unknown	34.8±11.8	70.2±11.8	22.9±11.8	82.2±11.8	43.0±14.4	71.1±14.4	43.5±14.4	59.9±11.8	45.2±11.8	98.4±13.6	6.7±13.6	-
Rearings: Proportion (%)												
Fungivores	47.4±4.8	41.1±4.8	42.3±4.8	46.2±4.8	35.3±5.9	49.4±5.9	47.9±5.9	40.7±4.8	47.6±4.8	42.2±4.6	46.2±4.6	-
Predators	20.9±2.8	18.7±2.8	25.7±2.8	13.9±2.8	20.4±3.5	24.2±3.5	14.8±3.5	16.9±2.8	22.7±2.8	14.6±2.7	25.0±2.7	-
Wood Borers	14.9±2.6	13.7±2.6	15.6±2.6	12.9±2.6	21.6±3.2	6.1±3.2	15.1±3.2	23.3±2.6	5.3±2.6	12.3±4.7	16.3±4.7	-
Scavengers	3.7±0.8	3.2±0.8	3.4±0.8	3.5±0.8	2.8±0.9	2.5±0.9	5.1±0.9	2.9±0.8	4.0±0.8	5.5±0.7	1.4±0.7	-
Unknown	13.1±1.9	19.1±1.9	12.9±1.9	19.3±1.9	13.7±2.4	17.8±2.4	16.9±2.4	16.1±1.9	16.2±1.9	25.3±2.2	6.9±2.2	-
Window-traps: Abundance												
Fungivores	134.2±29.4	258.3±29.4	175.7±29.4	216.8±29.4	204.9±18.8	202.0±18.8	181.7±18.8	-	-	-	186.5±19.8	205.9±19.8
Predators	118.9±49.0	150.5±49.0	179.5±49.0	89.9±49.0	216.0±37.7	89.6±37.7	98.5±37.7	-	-	-	130.8±19.1	138.19.1
Wood Borers	49.3±10.0	49.5±10.0	60.7±10.0	38.1±10.0	60.2±6.9	38.9±6.9	49.2±6.9	-	-	-	32.2±6.2	66.7±6.2
Scavengers	9.3±1.8	7.9±1.8	10.1±1.8	7.2±1.8	6.4±1.2	7.7±1.2	11.7±1.2	-	-	-	10.2±2.1	7.1±2.1
Unknown	34.4±5.6	26.6±5.6	30.6±5.6	30.5±5.6	34.2±2.1	31.8±2.1	26.7±2.1	-	-	-	25.9±5.6	35.2±5.6
Window-traps: Proportion (%)												
Fungivores	45.9±3	54.5±3	42.5±3	57.9±3	44.7±2.7	53.6±2.7	52.3±2.7	-	-	-	48.4±3.2	52.0±3.2
Predators	28.3±2.5	28.1±2.5	34.7±2.5	21.6±2.5	35.5±2.8	24.6±2.8	24.4±2.8	-	-	-	31.8±1.1	24.4±1.1
Wood Borers	11.7±1.5	10.0±1.5	12.7±1.5	8.9±1.5	10.9±0.6	9.6±0.6	11.9±0.6	-	-	-	8.8±0.8	12.9±0.8
Scavengers	3.2±0.4	1.7±0.4	2.4±0.4	2.5±0.4	1.2±0.6	2.9±0.6	3.2±0.6	-	-	-	2.8±0.3	1.9±0.3
Unknown	10.9±0.4	5.7±0.4	7.5±0.4	9.1±0.4	7.7±0.6	9.2±0.6	8.1±0.6	-	-	-	7.9±1.2	8.6±1.2

Table 3-6. Summary of diagnostics produced from detrended correspondence analysis of beetle species collected from *Populus* coarse woody material of three decay classes in old and mature boreal-mixedwood stands at Eureka River and Lac la Biche, Alberta from 1993-95. See text for details of analysis.

Collection method	**Taxa**	**Diagnostic**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**	**Total inertia**
Rearings	Saproxylics only	Eigenvalues (λ)	0.842	0.439	0.359	0.195	6.040
		Gradient Length	4.070	4.715	3.320	2.600	
		Total Cumulative Percent Variation explained by axis	13.9	21.2	27.1	30.4	
	All species reared	Eigenvalues (λ)	0.505	0.328	0.206	0.142	3.824
		Gradient Length	2.880	2.443	2.350	2.110	
		Total Cumulative Percent Variation explained by axis	13.2	21.8	27.2	30.9	
Window-traps	Saproxylics only	Eigenvalues (λ)	0.364	0.198	0.141	0.097	3.055
		Gradient Length	2.379	2.479	1.906	1.898	
		Total Cumulative Percent Variation explained by axis	11.9	18.4	23.0	26.2	

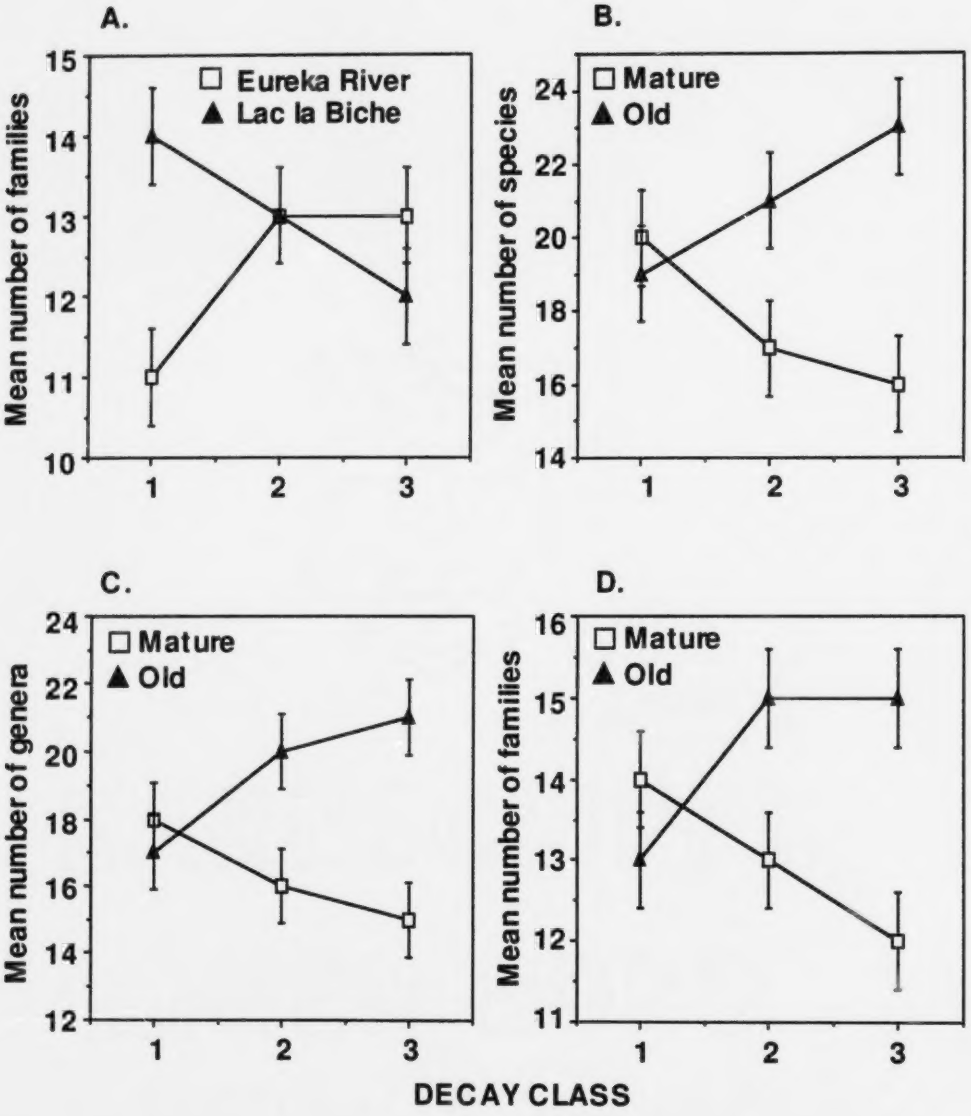

Figure 3-1. Summary of significant interactions of the mean number of taxa of saproxylic beetles collected with window-traps attached to *Populus* snags;

A. region x decay class interaction for family richness
B. age x decay class interaction for species richness
C. age x decay class interaction for genera
D. age x decay class interaction family richness.

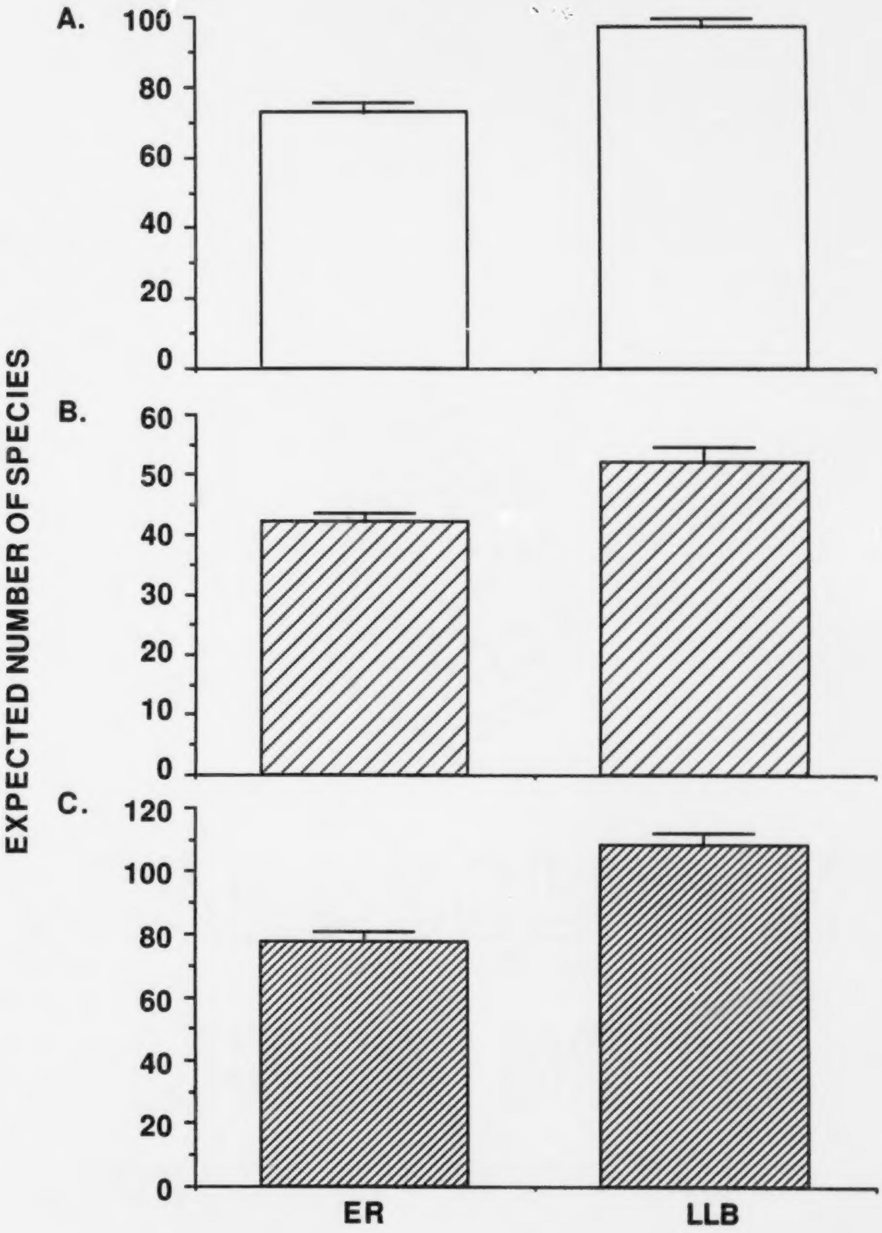

Figure 3-2. Rarefaction (mean± standard deviation) estimates of saproxylic beetle species richness from *Populus* CWM at Eureka River (ER) and Lac la Biche (LLB) based on rearing data;
A. 1993, subsample of 550 individuals;
B. 1994, subsample of 150 individuals;
C. 1993 and 1994 combined, subsample of 550 individuals.

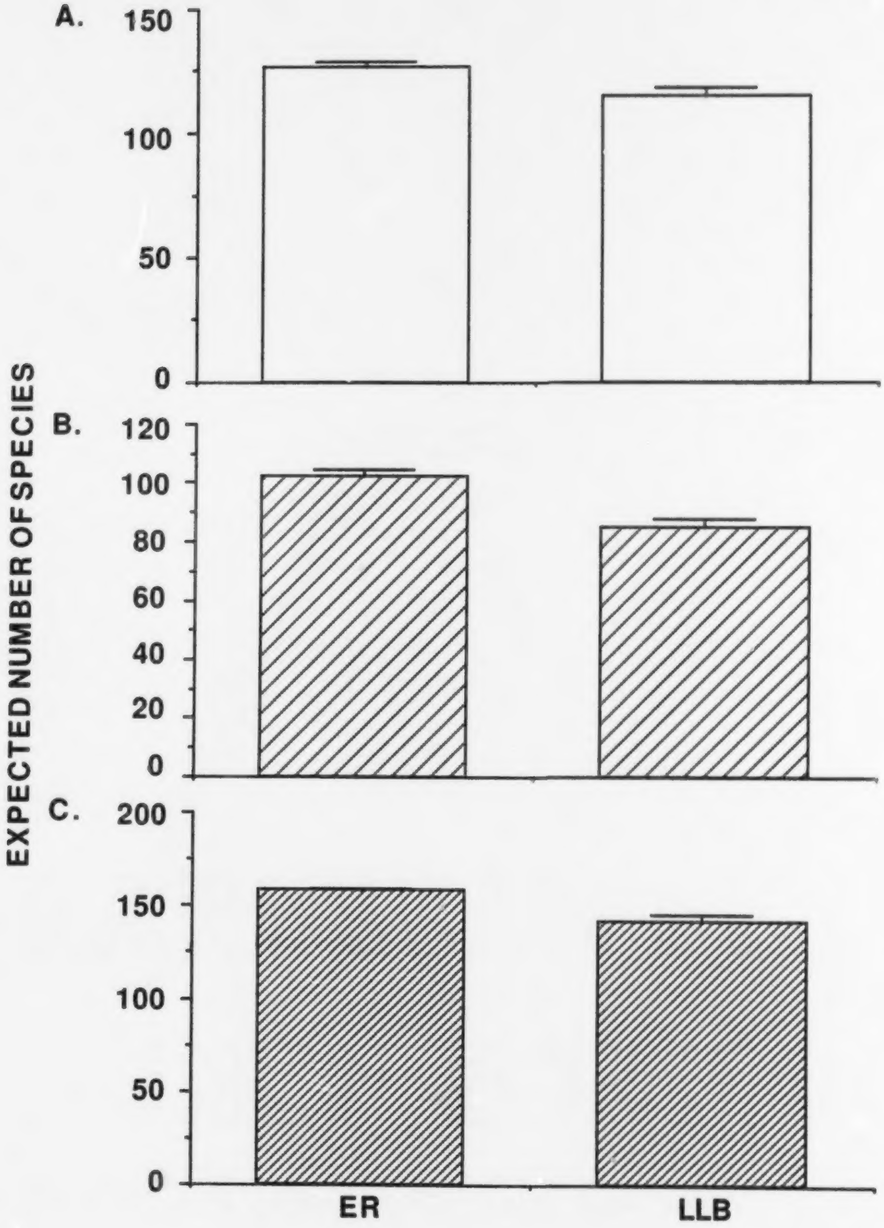

Figure 3-3. Rarefaction (mean± standard deviation) estimate of saproxylic beetle species richness in *Populus* CWM at Eureka River (ER) and Lac la Biche (LLB) based on window-traps;
A. 1994, subsample of 1600 individuals;
B. 1995, subsample of 1100 individuals;
C. 1994 and 1995, subsample of 3100 individuals.

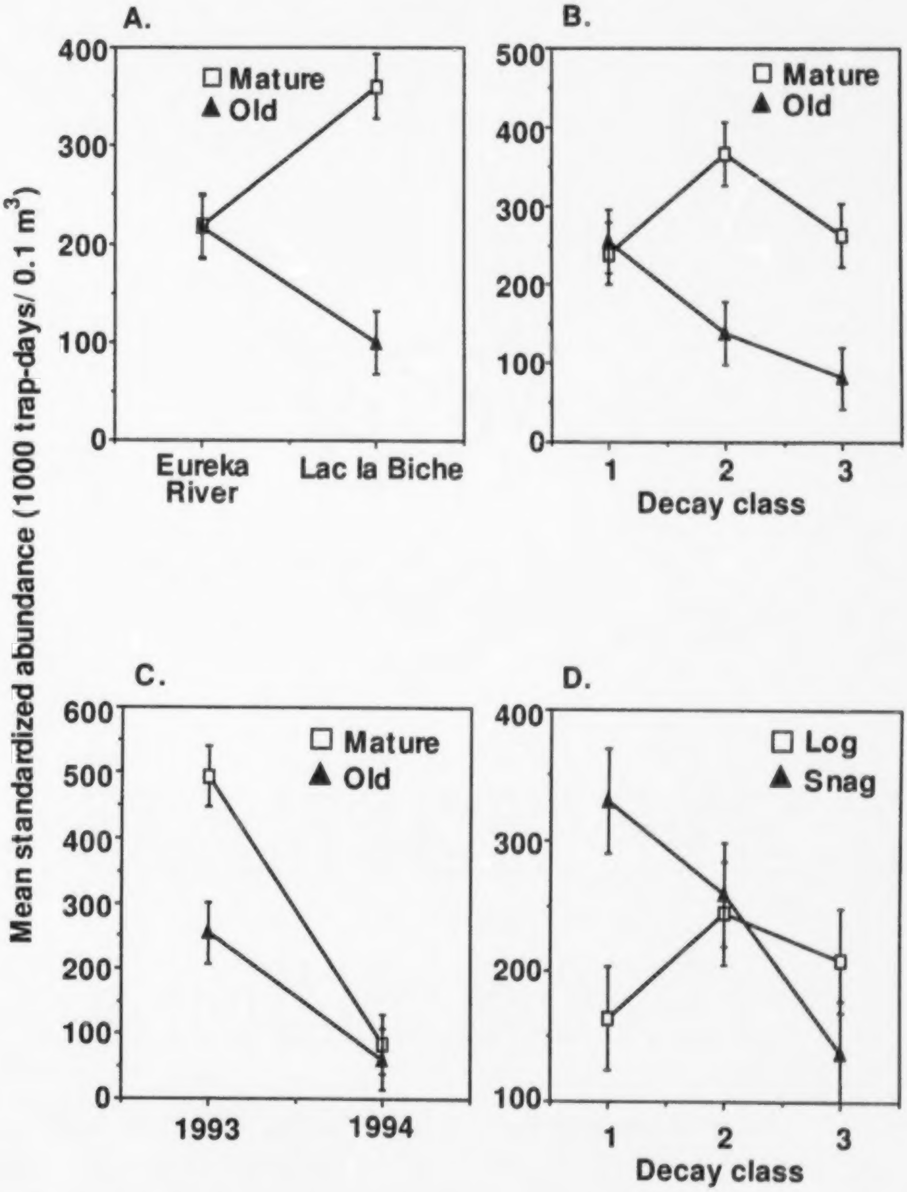

Figure 3-4. Summary of significant interactions of the mean standardized abundance of saproxylic beetles reared from bolts of *Populus* coarse woody material;

A. region x age interaction
B. age x decay class interaction
C. age x year interaction
D. decay class x type interaction.

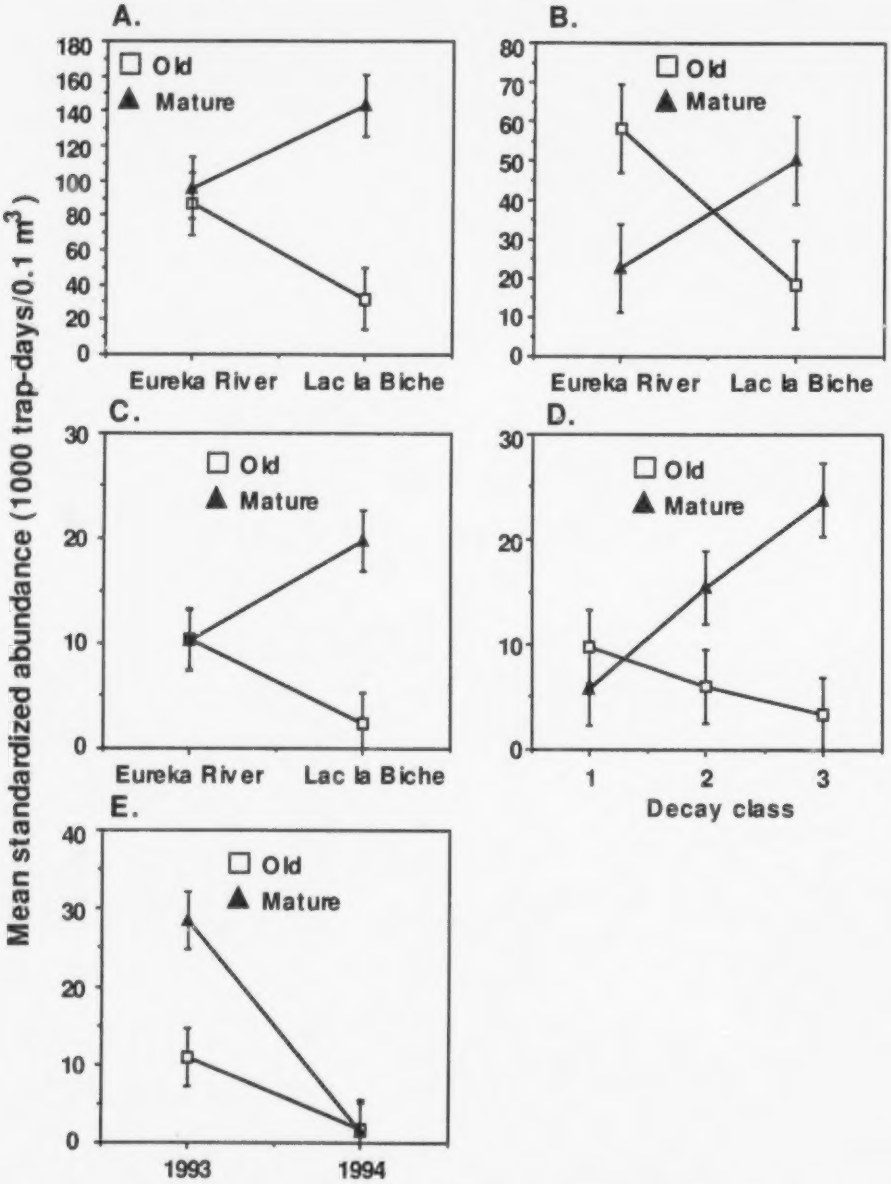

Figure 3-5. Summary of significant interactions of mean standardized abundance of trophic roles of beetles reared from *Populus* coarse woody material;

A. region x age interaction for fungivores;
B. region x age interaction for predators;
C. region x age interaction for scavengers;
D. age x decay class interaction for scavengers;
E. age x year interaction for scavengers.

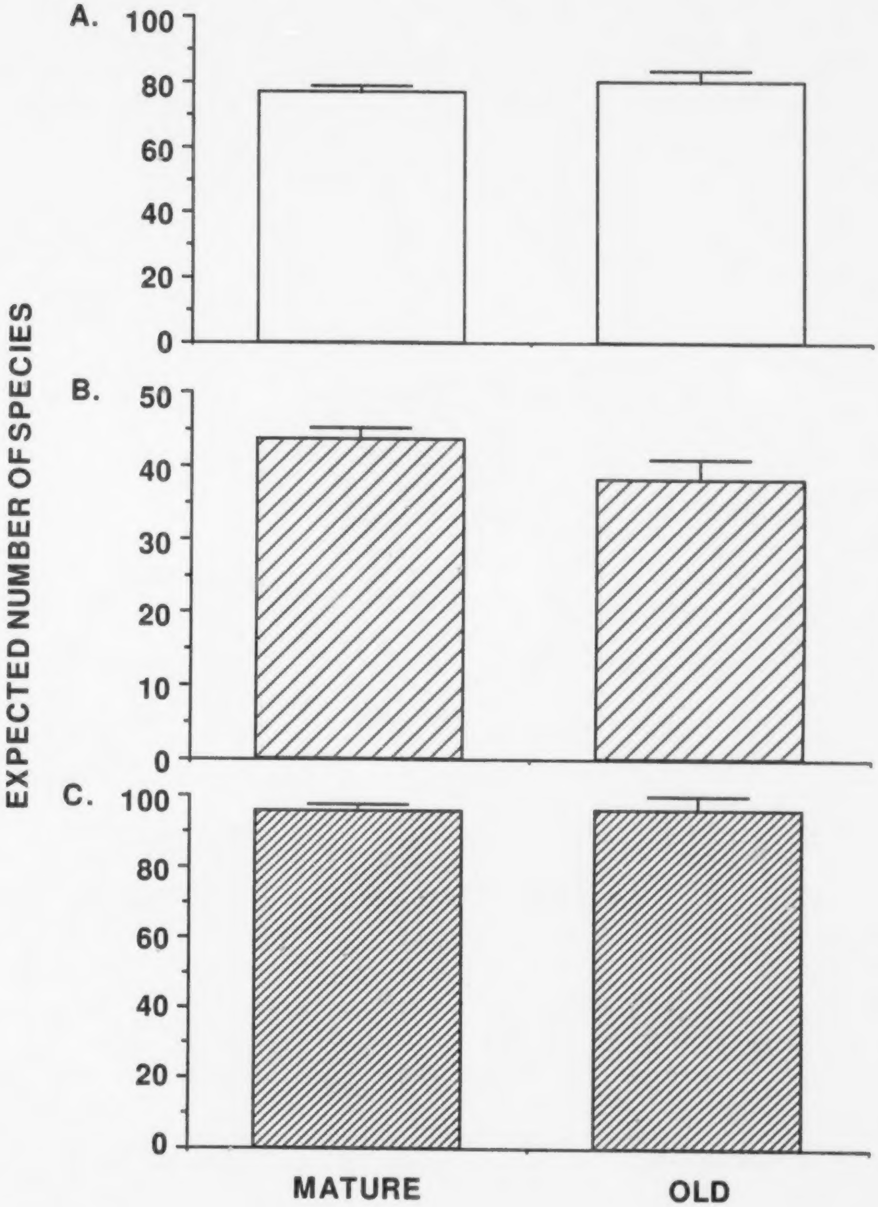

Figure 3-6. Rarefaction (mean± standard deviation) estimate of saproxylic beetle species richness in *Populus* CWM from mature and old age class stands based on rearings;
A. 1993, subsample of 450 individuals;
B. 1994, subsample of 100 individuals;
C. 1993 and 1994, subsample of 550 individuals.

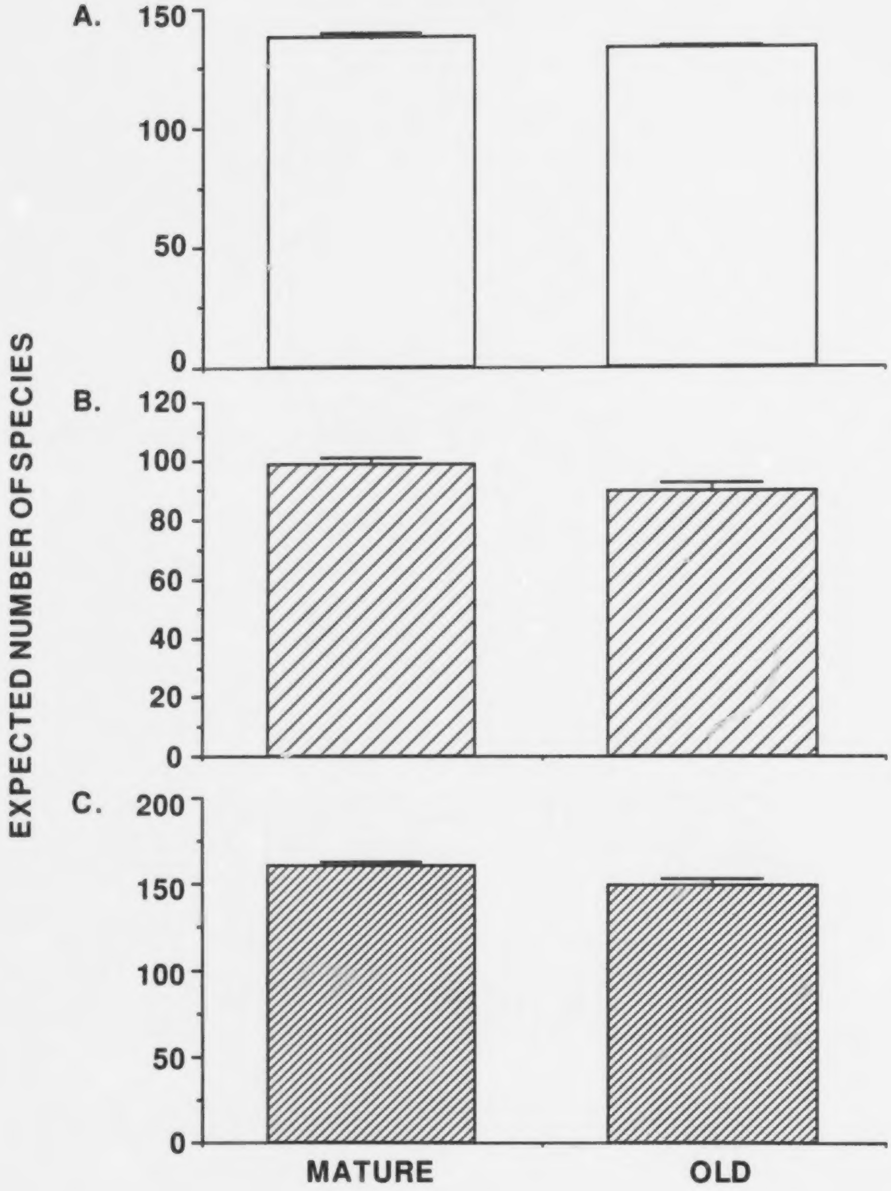

Figure 3-7. Rarefaction (mean±standard deviation) estimates of saproxylic beetle species richness in *Populus* CWM from mature and old age class forest stands based on window-traps;

A. 1994, subsample of 2100 individuals;
B. 1995, subsample of 1100 individuals;
C. 1994 and 1995, subsample of 3100 individuals.

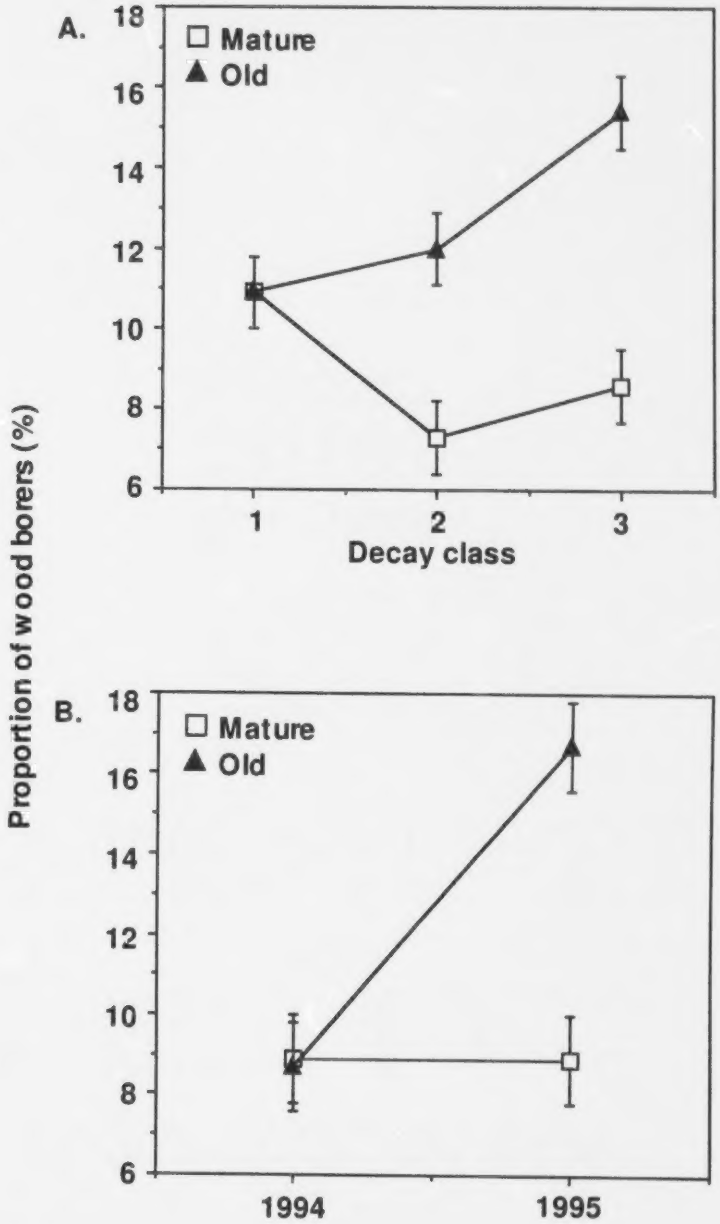

Figure 3-8. Summary of significant interactions for the proportion of wood borers collected with window-traps attached to *Populus* snags;
A. age x decay class interaction;
B. age x year interaction.

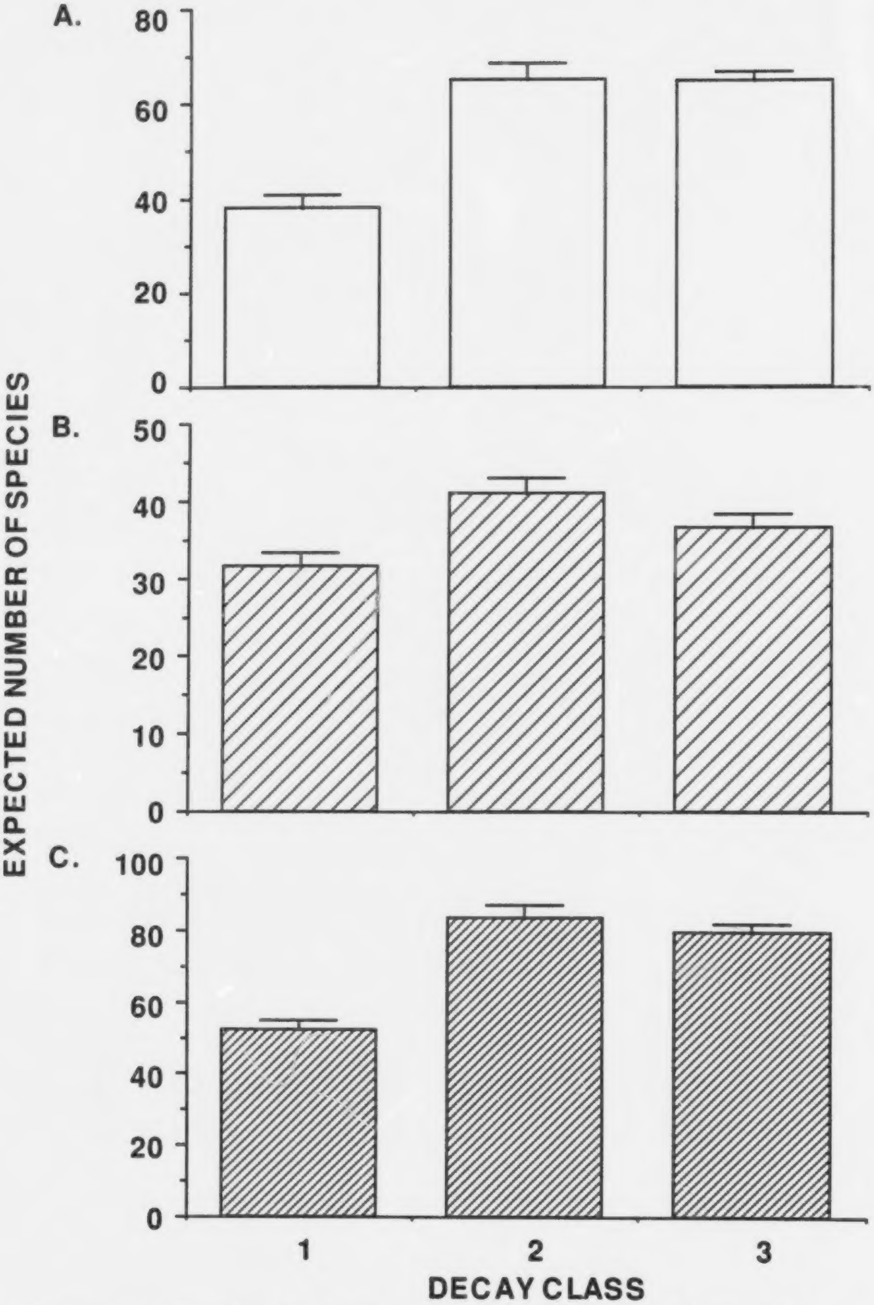

Figure 3-9. Rarefaction (mean± standard deviation) estimates of saproxylic beetle species richness from *Populus* wood varying in amount of decay, based on rearings;
A. 1993, subsample of 250 individuals;
B. 1994, subsample of 100 individuals;
C. 1993 and 1994, subsample of 350 individuals.

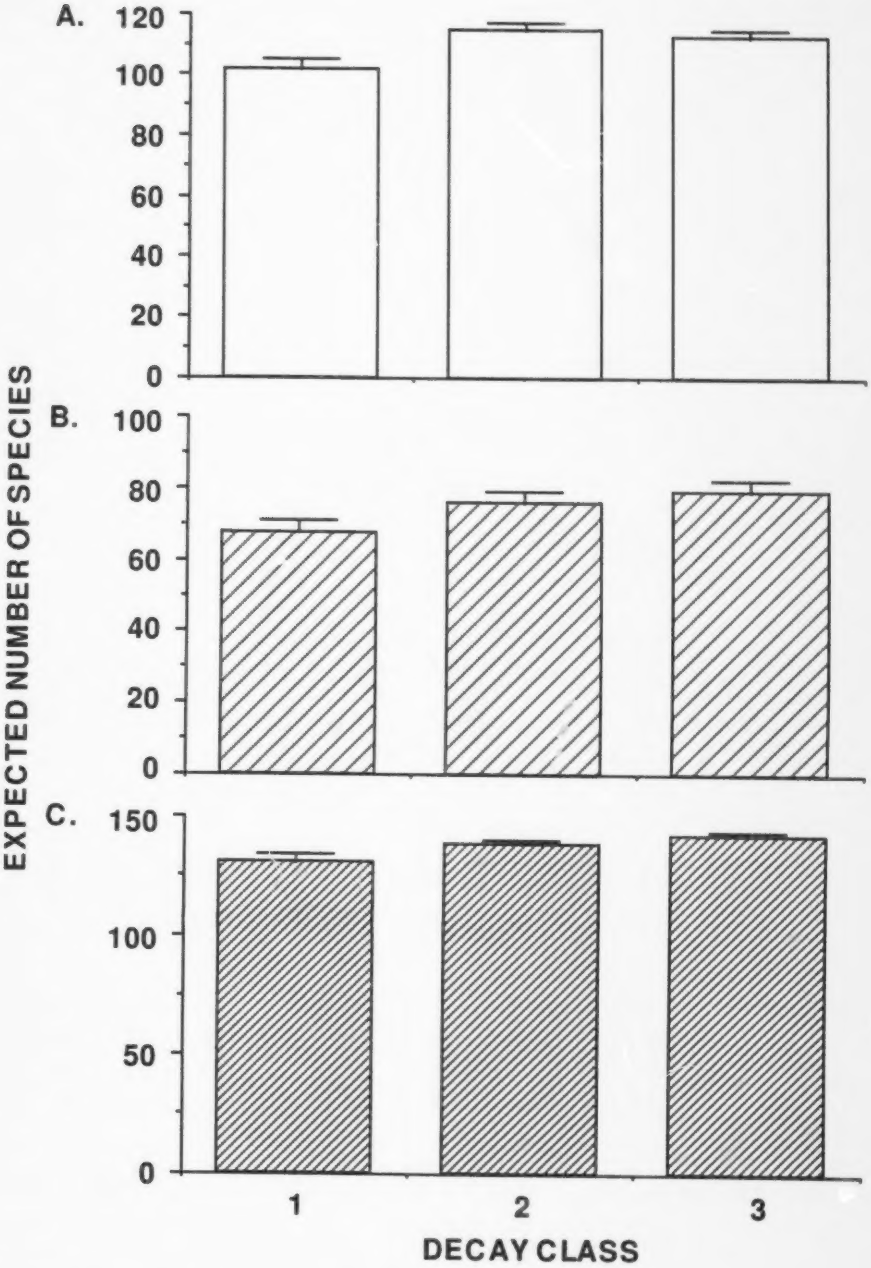

Figure 3-10. Rarefaction (mean± standard deviation) estimates of saproxylic beetle species richness from *Populus* snags varying in decay, based on window-traps;
A. 1994, subsample of 1100 individuals;
B. 1995, subsample of 550 individuals,
C. 1994 and 1995, subsample of 2100 individuals.

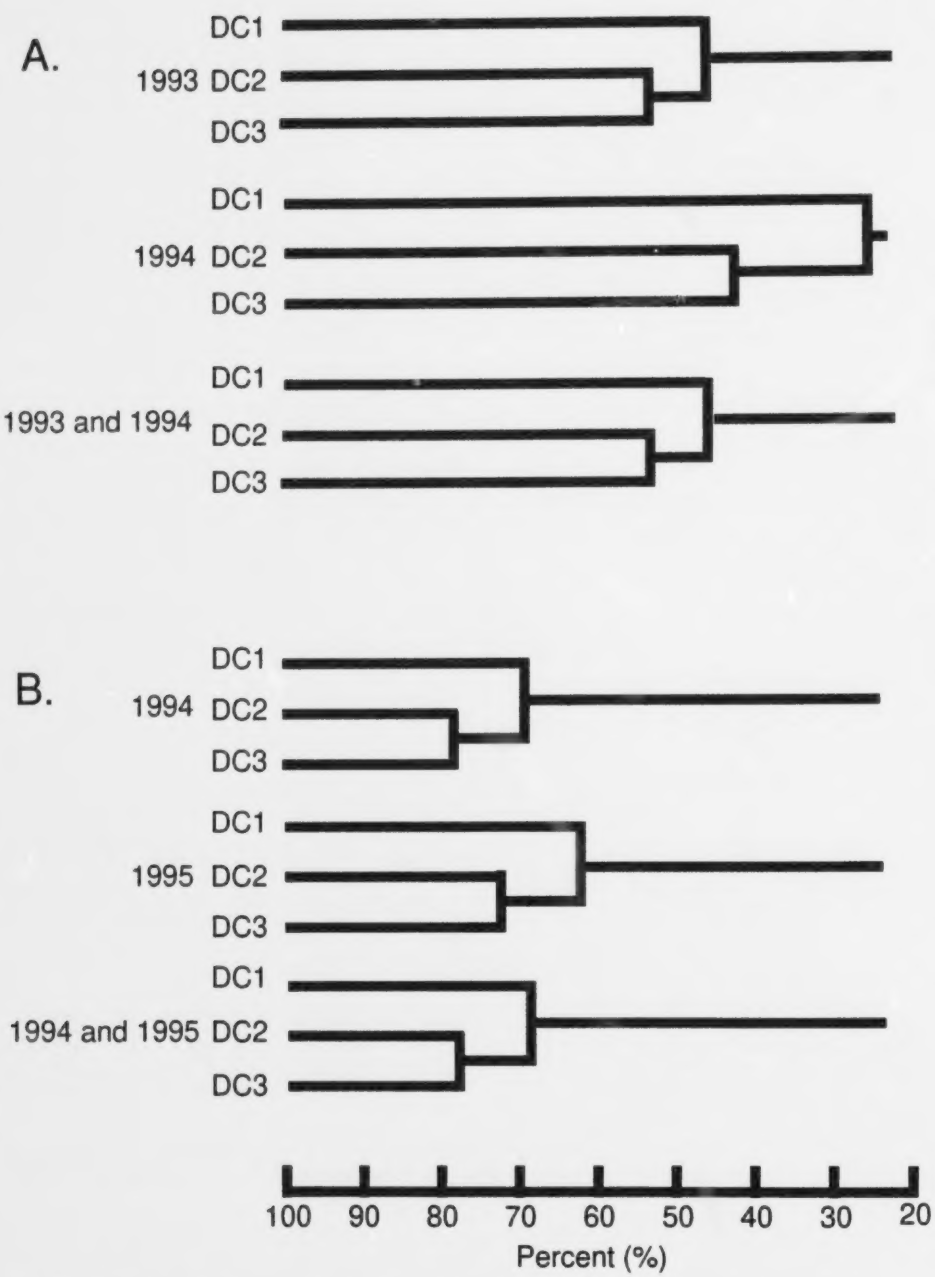

Figure 3-11. A cluster analysis of saproxylic beetle assemblages in coarse woody material of three decay classes, based on the Bray-Curtis index of percent similarity; A. data from rearings; B. data from window-traps.

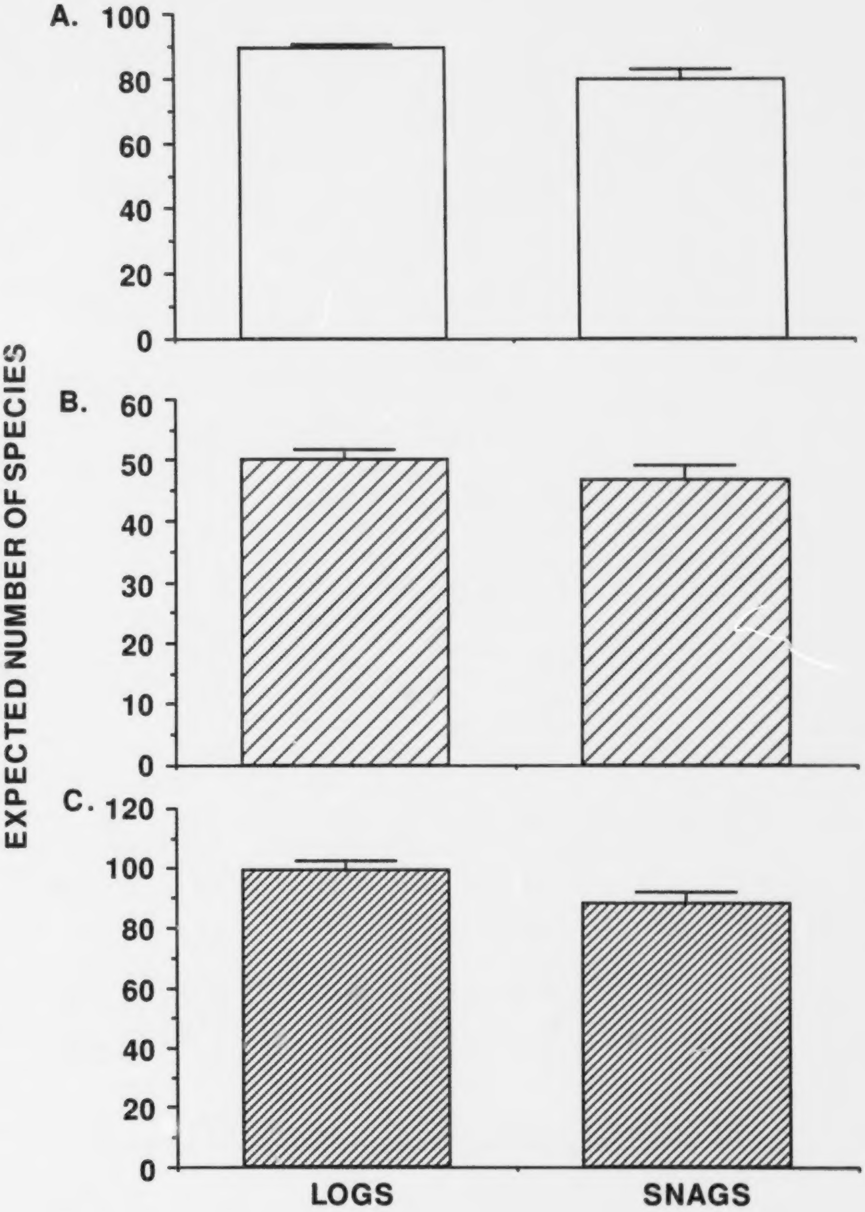

Figure 3-12. Rarefaction (mean± standard devaition) estimate of saproxylic beetle species richness of *Populus* snags and logs based on rearings;
A. 1993, subsample of 550 individuals;
B. 1994, subsample of 150 individuals;
C. 1994 and 1995, subsample of 550 individuals.

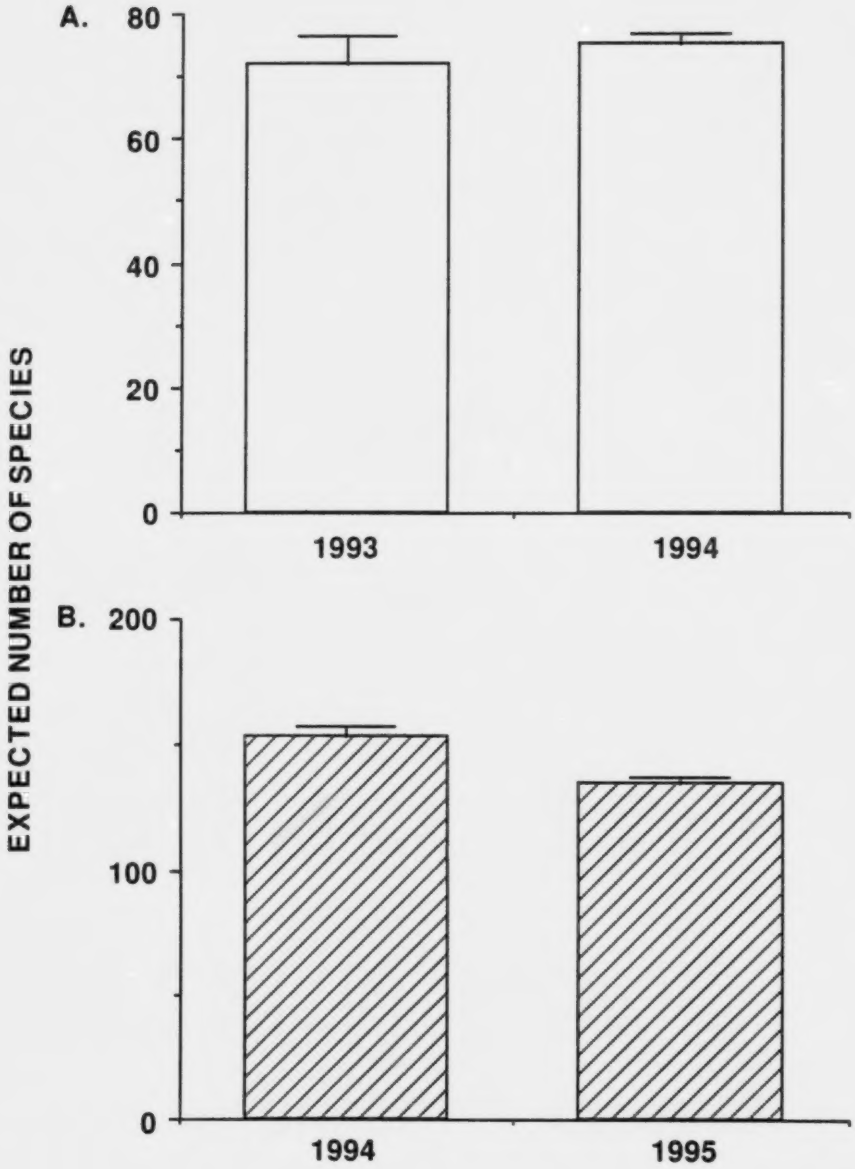

Figure 3-13. Rarefaction (mean± standard deviation) estimates of saproxylic beetle species richness from *Populus* CWM across sampling years;

A. data collected by rearings, subsample of 350 individuals;
B. data collected by window-traps, subsample of 3100 individuals.

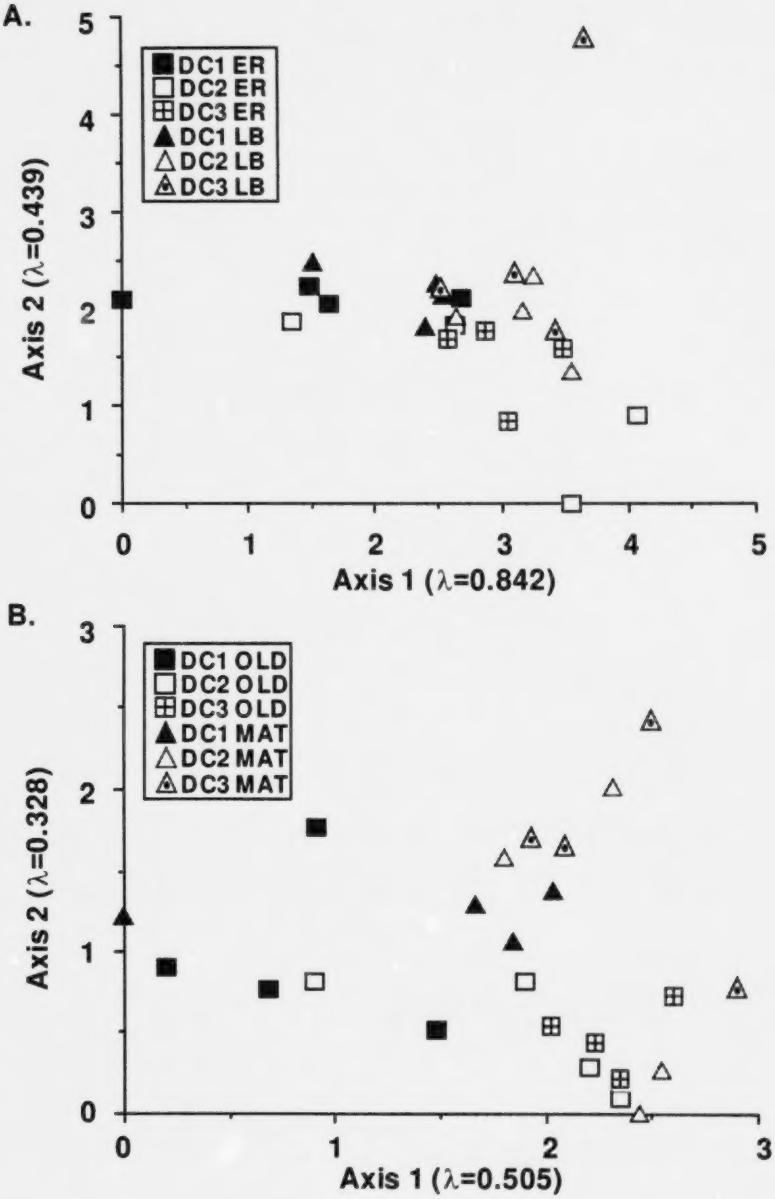

Figure 3-14. Detrended correspondence analysis of beetles collected by arthropod rearings from woody material in mature and old stands near Eureka River and Lac la Biche, Alberta;
A. includes only the saproxylic beetle community;
B. includes all beetles collected by rearings.

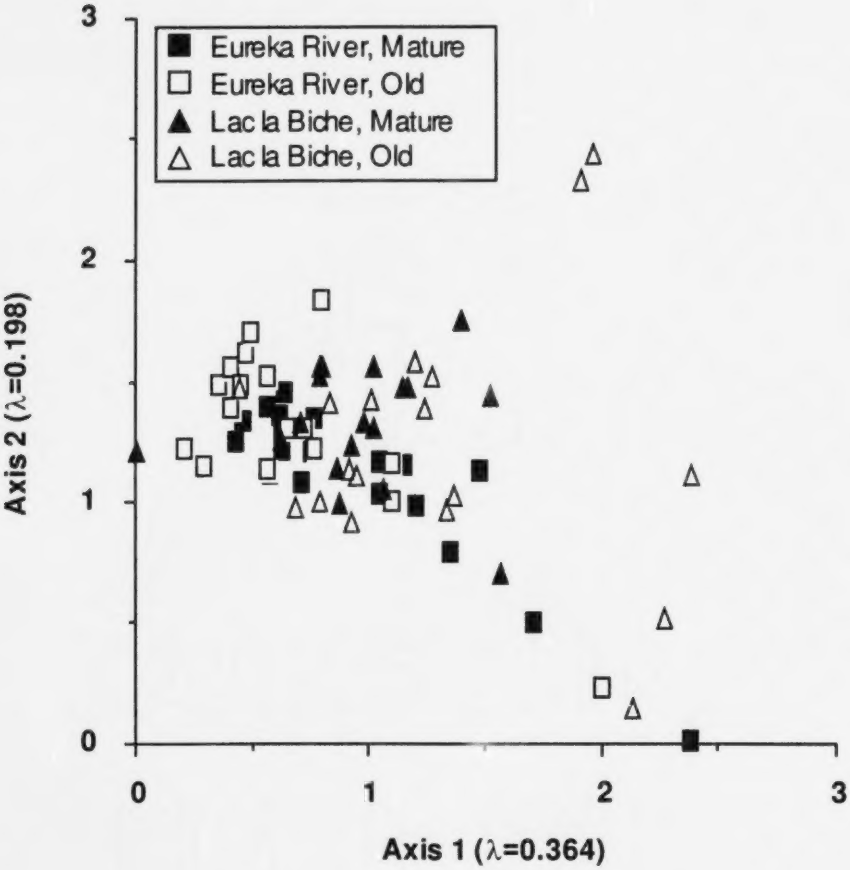

Figure 3-15. Detrended correspondence analysis of saproxylic beetles collected by window-traps from woody material in mature and old stands near Eureka River and Lac la Biche, Alberta, 1994-95.

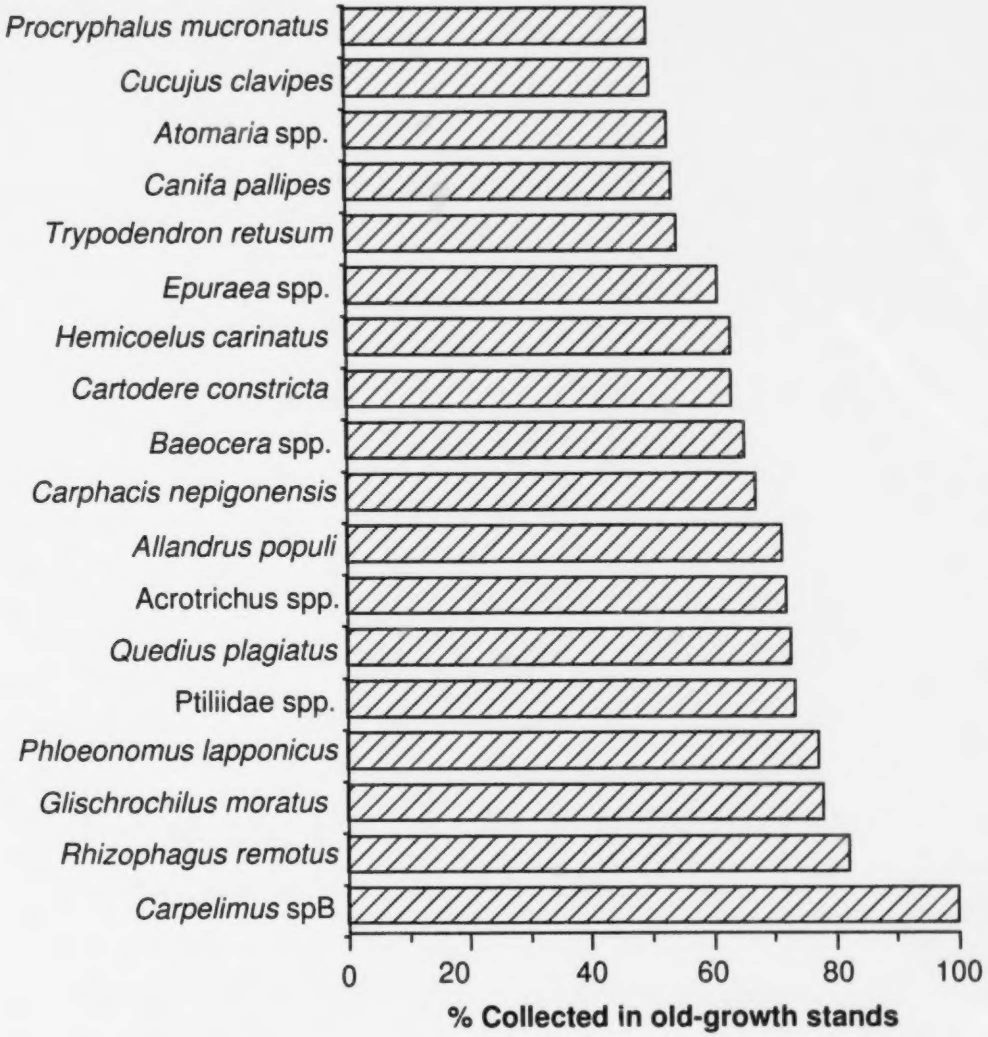

Figure 3-16. Old-growth dependence in beetles collected from insect rearings of wood cut from *Populus* snags and logs. See text for explanation of % collected in old stands, only species with old-growth dependency >50% shown in figure.

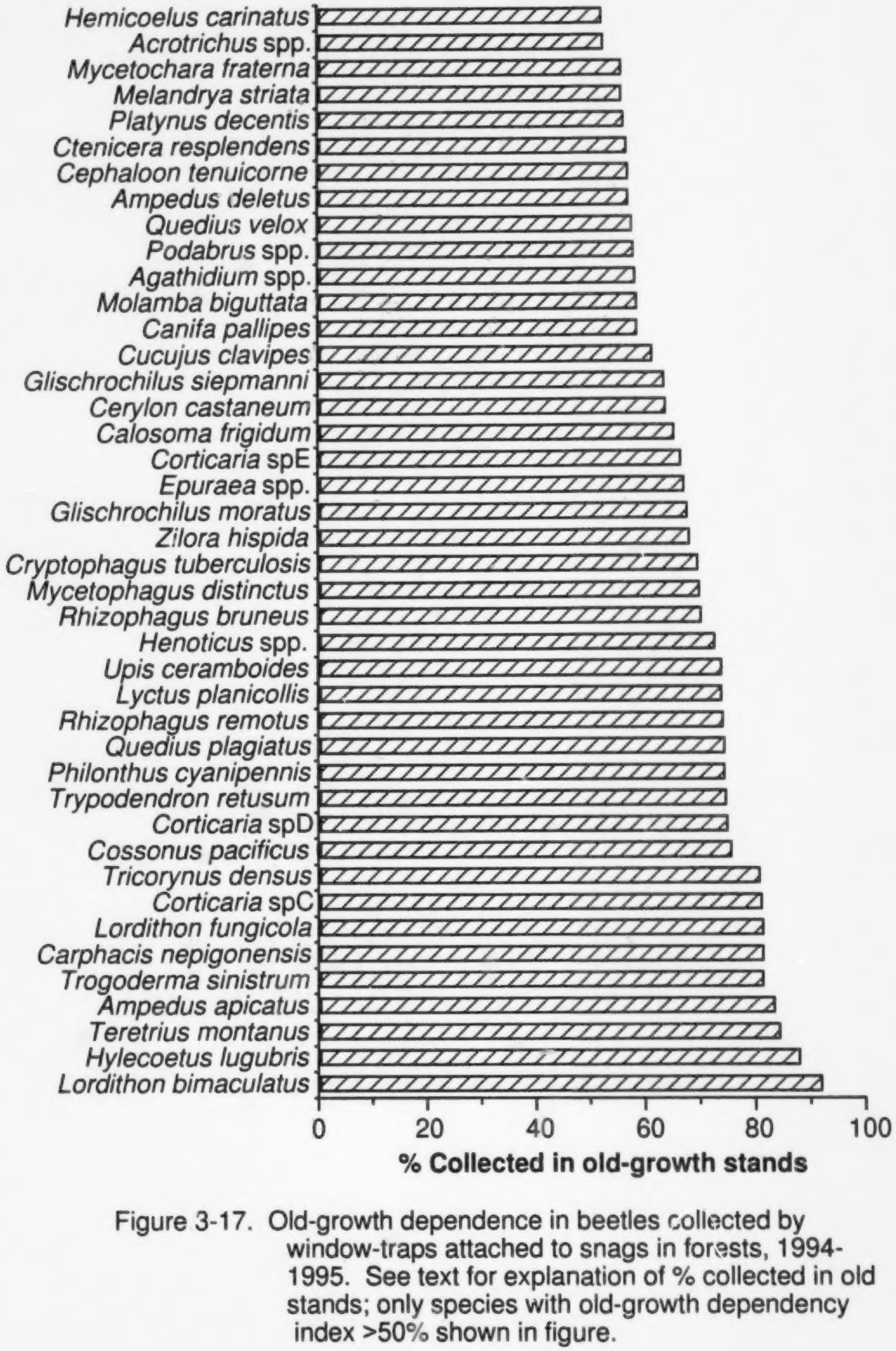

Figure 3-17. Old-growth dependence in beetles collected by window-traps attached to snags in forests, 1994-1995. See text for explanation of % collected in old stands; only species with old-growth dependency index >50% shown in figure.

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4. Immediate Effects of Forest Harvesting on the Saproxylic Beetle Assemblage Associated with *Populus* Snags

4.1 Synopsis

The effects of forest harvesting on beetle assemblages associated with *Populus* coarse woody material were studied in north-central Alberta. Saproxylic beetles from old, mature, and two-year-old harvested stands that were either old or mature before harvest, were sampled using modified window-traps attached to the boles of snags representing three decay categories. A total of 6747 beetles including at least 164 species were collected during the study. In general, old stands tended to have higher species diversity, regardless of whether they were forested or recently harvested. Harvested stands had higher species diversity and abundance compared to their forest counterparts. In addition, harvested old stands were more similar in faunal structure to old forest stands than to mature cutblocks, suggesting that faunal composition is not much affected for at least two years post-harvest. Management that leaves the appropriate range of habitats across the landscape, with sufficient connectivity between stands, should conserve saproxylic beetle assemblages.

4.2 Background and objectives

Much of western Canada is covered by a vast, relatively undeveloped wilderness of boreal-mixedwood forest. These forests are dominated by trembling aspen (*Populus tremuloides* Michaux) and white spruce (*Picea glauca* [Moench] Voss). Mixedwood forests in the prairie provinces make up approximately 20-40% of Canada's aspen resource (Peterson and Peterson, 1992). Within Alberta, mixedwood forests cover approximately 43% of the land area (Drew, 1988), making them the province's largest ecoregion.

About 29% of above ground biomass in Alberta's aspen-mixedwood forests is submerchantable timber and coarse woody material (Peterson and Peterson, 1992). Coarse woody material (CWM) consists of dead and dying trees (snags), logs, stumps, and associated root systems, and is one of the most important habitats for invertebrates in the forest ecosystem (Harmon et al., 1986; Speight, 1989; Väisänen et al., 1993; Siitonen and Martikainen, 1994). Saproxylic species, those which depend on dead wood, wood fungi, or the presence of other saproxylics, during some part of the life cycle (Speight, 1989), are profoundly affected by forest harvesting, agriculture, oil/gas exploration and other human activities (Heliövaara and Väisänen, 1984; Speight, 1989; Mikkola, 1991; Punttila et al., 1991; Warren and Key, 1991; Wilson, 1992). In Europe, an 80% drop in faunal diversity, mainly from the saproxylic community, has been attributed to centuries of forest harvesting and subsequent replanting of non-native conifer tree species (Speight, 1989).

Until recently, periodic wildfires and small scale harvesting of the pockets of white spruce were the major disturbances in Alberta's mixedwood forests. However, over the last two decades, harvest of aspen and poplar has become increasingly important economically, with total harvest increasing from 2% in 1971 to over 73% in 1994, and still growing (Peterson and Peterson, 1992; Alberta Land and Forest Service, 1994). This rapid increase in aspen utilization over a very short time has given rise to concerns over the effects of harvesting on biodiversity. Because aspen-mixedwood stands have not been previously exploited on a large scale, there is little empirical basis for anticipating the impacts and sustainability of this development (Navratil and Chapman, 1991).

Wilson (1992) argues convincingly that biological diversity is responsible for ecosystem integrity and resilience. Thus, sustainability of forest development demands an understanding of how forestry activities affect the distribution, abundance and diversity of the biota which comprise forest communities. Although plant and vertebrate components of mixedwood forests are relatively well known (Stelfox, 1995), there have been few studies of invertebrates in aspen forests (Spence et al., 1996, 1997), and how these assemblages respond to logging. In order to effectively conserve biodiversity in these forests, we must understand its structure, composition, and how it is affected by forest activities. This knowledge can then contribute to more ecologically sensitive practices that preserve biodiversity (Brussard, 1991; Probst and Crow, 1991).

The objective of this study was to assess how saproxylic beetle assemblages associated with *Populus* CWM respond to forest harvesting. This was achieved by examining faunal structure in old and mature forest stands of pyrogenic origin, and comparing them to two-year-old cutblocks that were either old or mature at harvest. Species richness, diversity, abundance and trophic structure are compared between forest and harvested stands. In addition, ordination analysis was used to investigate patterns underlying the distribution of saproxylic beetles from these stands.

4.3 Methods and materials

4.3.1 Study site

Arthropod communities from *Populus* CWM were sampled near Touchwood Lake, approximately 40 km east of Lac la Biche, Alberta (54° 51' N, 111° 27' W). This study site includes forest stands ranging in age from recently harvested to more than 100 years old. These stands are dominated (>75% canopy cover) by trembling aspen but also include a mixture of balsam poplar (*P. balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* B.S.P.), paper birch (*Betula papyrifera* Marsh.) and various willows (*Salix* spp.) in lesser amounts.

Two forest stands of each of two age classes were sampled. Old forest stands were characterized by having existed >100 years since last disturbance by fire, a canopy that was 20-27 m above the ground, and large diameter CWM ranging from 30-48 cm diameter at breast height (DBH). Mature forest stands had been undisturbed by wildfire for 50-65 years and had reached rotation age (*i.e.* harvesting age). The canopy formed a dense cover approximately 17-19 m above the ground, and CWM was smaller than in old stands, varying in size from 8.5-20 cm DBH.

I also sampled harvested stands, which were included in a patchwork layout of 30 ha cut blocks and 30 ha residual forest fragments (Stelfox, 1995). All stands were logged between December 1993 and March 1994. The two sampled 'old stand' cut blocks were 125 years of age when harvested, and contained CWM that ranged in size from 14-63 cm DBH after harvesting. The two 'mature stand' cutblocks were 51 years of age at harvest, and contained snags ranging in size from 7-22 cm DBH after harvest. All harvested stands retained a large volume of CWM on the ground, as well as individual and clumps of live trees throughout the cutblocks. Harvested stands were not scarified, but were left to regenerate naturally, mainly by suckers. All stands were within an area of homogeneous forest landscape of about 75 km^2.

Three wood decay stages were used to separate snags into 'minimally' decayed (decay class 1), 'moderately' decayed (decay class 2) and 'advanced' decayed (decay class 3; see Chapter 3 for decay class criteria). Because *Populus tremuloides* and *P. balsamifera* CWM are often difficult to identify, especially as snags of large diameter and in states of advanced decay, beetle data is not partitioned by tree species.

4.3.2 Study design and data collection

Window-traps modified from Käila (1993), were used to sample insects flying to and from snags (see Chapter 2). Two window-traps, one with the top of the window at breast height (ca. 1.3 m) and the second with the top of the window at ca. 2.0 m were placed on each snag. The direction of both traps on each snag were the same, but randomized over the study. Three snags in each of the three decay classes were sampled in each stand, except for one 'old' cutblock where only decay classes 1 and 3 were sampled because decay class 2 snags were absent. Therefore, eighteen window-traps were set out in each of the four forest stands and three of the harvested stands, with the remaining 'old' cutblock having only 15 window-traps. Insects were collected biweekly from 02 May-28 August, 1995.

4.3.3 Data analyses

Only saproxylic beetles associated with *Populus* CWM were included in analysis, as listed in Table 4-1. Saproxylic beetles are herein defined as species which use dead wood and its associated biota for food or reproduction. This includes predators, scavengers, fungivores, xylophages and phloeophages. Because sampling effort was not identical across stands, catches from window-traps were standardized to 1000 trap-days.

Mean number of taxa collected over a season and their mean standardized abundance were analyzed using a 3-way analysis of variance (ANOVA, proc GLM) in SAS (Steel and Torrie, 1980). The main effects in the ANOVA were stand age, stand type (i.e., forest or harvest), and snag decay class. Parametric analysis was also used to compare trophic structure of beetle assemblages from CWM. Beetle taxa were assigned to one of four trophic roles, predator, fungivore, wood borer, and scavenger based on the known habits of the predominant life stage found in dead wood. All xylophagous and phloeophagous taxa were included in the wood borer category. Taxa for which trophic role was not known or uncertain were classified as unknown. Mean standardized abundance and proportion of overall standardized abundance represented by each trophic role was compared and tested using GLM in SAS, similar to the model described above. Full ANOVA tables are presented in Appendices 7-9.

In addition to comparing the mean number of taxa, species diversity was measured three ways to minimize bias when using a single method (Grassle et al, 1979; Krebs, 1989). First, to correct for sampling errors and for uneven catches, I calculated an unbiased estimate of species richness using rarefaction (Sanders, 1968; Hurlbert, 1971). Rarefaction predicts the number of species in a subsample taken from the original sample based on probabilities calculated from observed species abundance. Thus, rarefaction is a measure of diversity that can be compared across samples standardized for total capture. The Shannon-Wiener index (H'), is based on the assumptions that individuals are randomly sampled from an infinitely large population, and that all species are represented in the sample (Pielou, 1975; Magurran, 1988). This method is easy to calculate and its wide use in the literature facilitates comparisons with other communities (Magurran, 1988). Thirdly, the Berger-Parker index (d') is a dominance measure, simply the inverse of the abundance of the most dominant species in a sample divided by the total abundance in the sample (Magurran, 1988). In general, the higher the d' the lower the ratio of the most abundant species to the total and the more even the distribution.

A FORTRAN program, similar to that of Krebs (1988) but modified to run on the VAX system at the Northern Forestry Center (Canadian Forest Service) was used to calculate rarefactions, the program StatEcol (Ludwig and Reynolds, 1988) was used to calculate the Shannon-Wiener index, and the Berger-Parker index was calculated directly from Excel spreadsheets. I used cluster analysis of Bray-Curtis percent similarity measures with group averaging as the weighting procedure in the program StatEcol (Ludwig and Reynolds, 1988), to compare relationships of beetle assemblages among different samples and sites.

To better understand factors influencing the abundance pattern of each species, the standardized abundance of taxa in each sample matrix was subjected to ordination using detrended correspondence analysis (DCA) (Hill, 1973; Hill and Gauch, 1980; Gauch, 1982; ter Braak, 1987) using the computer program CANOCO (ter Braak, 1987). Detrended correspondence analysis is an indirect gradient technique which constructs axes that maximize the variation of each species abundance across samples, and in doing so helps to identify factors that most influence the observed species distributions. Although I tested several ordination methods, such as principal components analysis and correspondence analysis (ter Braak, 1987), DCA was the ordination method that maximized the spread (variation) in the data points, while at the same time not creating axes based only on a few species. Rare species (species with frequencies less than the frequency of the commonest species divided by five) were downweighted to a score of one, to reduce their influence on the ordination. Only q-matrix (ordination based on the sample unit matrix), providing sample unit ordinations, are presented.

4.4 Results

4.4.1 Effects of stand age

A total of 6747 saproxylic beetles, representing at least 164 species, were collected from the four forested and four harvested stands near Lac la Biche in 1995 (Table 4-1). Of these 6, 3, 25 and 22 species were unique to old forests, mature forests, 'old' cutblocks and 'mature' cutblocks, respectively, 24 of these species were considered rare (Table 4-2). A total of 100 taxa were collected in forest stands, and of these 18 were collected only in mature stands and 28 collected only in old stands; whereas, of the 153 taxa collected in cutblocks, 29 were collected only in 'mature' cutblocks, and 41 were collected only in 'old' cutblocks (Table 4-1).

Six taxa, *Siagonum punctatum* LeC., *Endecatomus rugosus* (Rand.), *Upis ceramboides* (L.), *Cortinicara gibbosa* (Herbst), *Dolichocis manitoba* Dury and *Platydema americanum* Cast. and Brul., were collected only from both old forest and 'old' cutblocks (Table 4-1). However, only 2 species, *Cercyon pygmaeus* (Ill.) and one species of *Enicmus*, were collected only from mature forests and 'mature' cutblocks (Table 4-1).

There was no effect of stand age on the mean number of species, genera, families or standardized abundance (Table 4-3). However, both

Shannon-Wiener and Berger-Parker diversity indices (Table 4-4) and rarefaction estimates of species richness (Figure 4-1) were slightly higher for old forest stands than for mature forest stands. Although all four harvested stands were cut in the same year, and thus technically the same age (two years) at time of sampling, stands which were 'old' when harvested still exhibited higher diversity and species richness than stands mature at harvest (Table 4-3 and Figure 4-1).

Cluster analysis showed that saproxylic beetle assemblages in old forests were more similar to 'old' cutblocks than to mature forests (Figure 4-2A).

Trophic structure of beetle assemblages was significantly influenced by stand age. The mean standardized abundance of fungivores was significantly higher in mature forests (df=1, F=7.43, P=0.0527) and mature cutblocks than in old forests and old cutblocks; whereas, the mean standardized abundance of wood borers was significantly higher in old stands and old cutblocks (df=1, F=12.32, P=0.0247) compared to mature stands and mature cutblocks (Table 4-5). These data are also reflected in proportional abundance of trophic roles. The proportion of fungivores was significantly higher in mature forests and mature cutblocks (df=1, F=36.81, P=0.0037) than old stands and old cutblocks; whereas old stands and old cutblocks had a significantly higher proportion of predators (df=1, F=11.05, P=0.0293) and wood borers (df=1, F=28.87, P=0.0058) than their mature counterparts (Table 4-5).

4.4.2 Effects of harvesting

Cutblocks had a significantly higher number of species (df=1, F=33.15, P=0.0045), genera (df=1, F=33.71, P=0.0044), families (df=1, F=28.81, P=0.0058), and standardized abundance (df=1, F=22.88, P=0.0088) than forest stands (Table 4-3). Similarly, the Shannon-Wiener and Berger-Parker indices (Table 4-4), as well as the rarefaction estimates of species richness (Figure 4-1) were higher for cutblocks than for forest stands. A total of 11 taxa were present in forest stands but not present two years post-harvest (Table 4-1); whereas, a total of 64 taxa, including two species of Anthribidae, and nine species of wood borers in the families Buprestidae, Cerambycidae, Curculionidae and Scolytidae, were present in harvested stands but absent from forests (Table 4-1).

Harvested stands had a significantly higher mean standardized abundance of fungivores (df=1, F=46.49, P=0.0024), wood borers (df=1, F=26.28, P=0.0069), and scavengers (df=1, F=29.71, P=0.0055) than did forest stands (Table 4-5). However, trophic structure was relatively unaffected by harvesting, except for the proportion of scavengers, which were significantly more abundant (df=1, F=13.93, P=0.0202) in harvested stands (Table 4-5).

4.4.3 Effects of decay class

Although there were no differences in taxon diversity among decay classes (Tables 4-3 and 4-4; Figure 4-3), mean standardized abundance was significantly higher (df=2, F=7.93, P=0.0159) in decay class 1 than the other two decay classes (Table 4-3). In addition, 19, 13 and 9 taxa were unique to decay class 1, 2, and 3 snags in forests, and none of these species were similarly unique to the respective decay classes in harvested stands (Table 4-1).

In general, all decay classes from forests (old and mature) tended to cluster together as more similar than decay classes from harvested stands (Figure 4-2B).

Mean standardized abundance for fungivores was significantly higher (df=2, F=5.95, P=0.0309) in decay class 1 wood than from the other decay classes (Table 4-5). Trophic structure, on the other hand, was relatively similar between decay classes except for the proportion of scavengers, which were relatively more abundant (df=2, F=9.85, P=0.0092) in decay class 3 snags (Table 4-5).

4.4.4 Ordination analysis

Sample unit DCA of saproxylic beetle groups collected with window-traps is presented in Figure 4-4. The first DCA axis separates sample units based on stand type, with forested stands closer to the left of the plot and harvested stands toward the right (λ=0.315). The second DCA axis separates the sample units based on stand age with mature stands towards the bottom of the second axis and older stands towards the top of the second axis (λ=0.179). However, only 17.4% of the variation is explained by these two axes, and combined with the low eigenvalues, suggests that many abiotic and biotic factors influence the distribution of saproxylic beetles across the landscape.

4.5 Discussion

4.5.1 Influence of harvesting on saproxylic beetle assemblages

Clearly, the composition of saproxylic beetle assemblages changes somewhat following forest harvest. Although trophic structure was unaffected by harvesting (Table 4-5), species richness, diversity and abundance were higher in harvested stands (Tables 4-3, and 4-4; Figures 4-1 and 4-3). This is a common pattern observed for other forest arthropods in other forest types in North America (Vlug and Borden, 1973; Seastedt and Crossley, 1981; Lenski, 1982; Bird and Chatarpaul, 1986; Jennings et al., 1986; Niemelä et al., 1993a; Setälä and Marshall, 1994; Greenberg and Thomas, 1995) and Europe (Arnoldi and Matveev, 1973; Szyszko, 1983; Helle and Muona, 1985; Biström and Halme, 1988; Niemelä et al., 1988; Duelli et al., 1990; Stokland, 1991; Punttila et al., 1991; Halme and Niemelä, 1993; Niemelä et al., 1993b). A similar pattern is observed among understory plants (Corns and La Roi, 1976; Oliver, 1981; Outcalt and White, 1981). It has been postulated that the increase in species richness of carabid beetles in recently harvested stands is due to the influx of open habitat specialists (Niemelä et al., 1993a, 1993b). Among the 17 species of carabids collected during this study, 9 are considered open habitat specialists, including *Pterostichus adstrictus* Esch., *Trichocellus cognatus* (Gyll.), *Bembidion* spp., and *Amara* spp., and these were collected predominantly in harvested stands (Table 4-1).

The predominance for higher species diversity in harvested stands may also be associated with changes in the physical characteristics of stands following harvesting as suggested by ordination (Figure 4-4). Often, abiotic factors such as temperature and air movement increase in stands after harvest (Matlack, 1993; Chen et al., 1995; Murcia, 1995). Increased air and ground temperatures may be attractive to 'pyrophilous' species such as *Agonum* spp., *Dicerca* spp., and *Pterostichus* spp. (Evans, 1971; Richardson and Holliday, 1982; Holliday 1991, 1992), which can detect increased temperatures from considerable distances. Also, increased air movement through open cutblocks may 'carry' pioneer species into these areas. The action of wind has been shown to be quite important for the re-establishment of species on islands and mountains following disturbance (Wilson, 1992).

Many beetle species may be more common in harvested stands because of the large amount of CWM remaining on site after harvest. Volatiles emanating from weakened and recently dead wood are attractive to many bark- and wood boring species (Chapman, 1963; Schowalter et al., 1992). Of the 19 phloeophagous and xylophagous species collected, 11 were collected exclusively in harvested stands. Also, *Rhizophagus dimidiatus* Mann. and *R. remotus* LeC., specialist predators on bark beetles, were collected primarily in harvested stands (Table 4-1). Undoubtedly, the fungi colonizing *Populus* wood also give off volatiles attractive to fungivorous insects, as is known for other species of wood (Witcosky et al., 1987; Hedlund et al., 1995; Jonsell and Nordlander, 1995). Therefore, the large volume of decaying CWM left on site after harvest may explain why about half of the 60 species of fungivores were collected mainly in cutblocks (Table 4-1).

It should not be concluded that the many woodborer, fungivorous and predatory taxa collected exclusively in harvested stands do not also occur in forests. Most of these species are likely rare and localized in forests, so substantial effort may be required to detect them. In fact, all but two species, *Tropideres dorsalis* (Thunberg) and *Glischrochilus vittatus* (Say), have been collected in aspen-mixedwood stands near Lac la Biche or Eureka River, Alberta (see Chapter 3). Harvested stands may thus serve as 'islands' which serve to attract and concentrate open habitat specialists for some period of time following harvest. The suitability of the wood as resources for wood borers will decline with time as the wood deteriorates. These species will then likely move into adjacent forest or recently harvested stands. But, as this wood continues to decay it may become more attractive to species specializing on heavily decayed wood (see Chapter 3). Only longer term chronosequence studies will elucidate these relationships.

4.5.2 Effects of stand age and decay class

It is interesting that differences in beetle assemblages between mature and old stands seem to remain, to some degree, for at least two years after harvest. Diversity (Table 4-4) and rarefaction estimates of species richness were higher for old forest stands and cutblocks than their mature counterparts (Figure 4-1). Cluster analysis revealed that 'old' cutblocks were more similar to old forest stands than to 'mature' cutblocks (Figure 4-2A). It may be that saproxylic insect assemblages survive harvesting and remain relatively intact two years post-harvesting; only 11 of the 100 species found in forest stands were absent from harvested stands (Table 4-1).

Higher species richness in older forest stands and cutblocks may reflect the size of CWM in these stands. Snags were considerably larger in diameter in 'old' forests and cutblocks (30-63 cm DBH) than in 'mature' forests and cutblocks (8.5-22 cm DBH). Väisänen et al. (1993) showed that the presence of saproxylic beetles in dead pine depended on trunk diameter, bark area, and stand age. In addition, there is a positive correlation between CWM size and wood moisture content (Brackebusch, 1975; Harmon et al., 1986). Therefore smaller diameter snags may lose certain micro-habitats (e.g. fungi) available to saproxylic beetles much more quickly than large snags.

Emigration of beetles from adjacent residual forested blocks may also aid in maintaining the original assemblage in cut blocks. Only long term monitoring can determine how long assemblage structure remains intact. If the fauna contains many species that prefer older forests, assemblage integrity can be expected to degenerate as these species disappear. For instance, it has been shown that several species of carabid beetles that have an affinity for old-growth lodgepole pine forests may survive for at least two years in newly harvested stands, but disappear by nine years post harvest (Niemelä et al., 1993a). However, Ås (1993) suggests that in areas of intensive forestry that have patches of CWM that have not become isolated islands, wood inhabiting species do not become split up into separate populations, and concludes that CWM in harvested areas facilitates movement between fragments preventing populations from becoming isolated. Therefore, current harvesting practices which include leaving most standing and fallen CWM as well as small clumps of living trees will serve as a source of new snags may help the survival of saproxylic arthropod assemblages.

Trophic structure of beetle assemblages differed greatly between mature and old stands (Table 4-5). The proportionately higher abundance of fungivores and lower abundance of predators in mature stands compared to old is similar to that reported in Chapter 3. This study also showed that wood borer abundance was proportionately higher in old stands. This may be a numerical response to the greater volume and size of CWM in old-growth forests.

The distribution of beetles among decay classes was not affected much by harvesting. The higher standardized abundance of beetles in decay class 1 (Tables 4-3 and 4-5) reflects the large volume of new CWM in harvested stands. Interestingly, saproxylic beetles collected from decay class 1 snags in old forest stands were more similar to decay class 1 snags in 'old' harvested stands than to other decay classes in old forests; however, all mature forest decay classes clustered together (Figure 4-2B). Wallace (1953) also showed that bark beetles and related groups were the first to colonize new dead wood, and that this pattern was more clearly defined in harvested stands than in forests. This finding helps support the argument that CWM in harvested stands may concentrate certain species following harvesting.

4.5.3 Implications for beetle conservation

It has been suggested that the best means for preserving regional biodiversity is conservation of maximum habitat diversity (Niemelä et al., 1988; Speight, 1989; Mikkola, 1991; Harris and Silva-Lopez, 1992). In order to develop land management strategies that are ecologically sensitive, it is necessary to understand how forest invertebrate species vary across the landscape, and how they respond to large scale disturbance.

The data from this study suggests that conservation of the saproxylic insect fauna in the boreal mixedwood can be achieved through a 3-part strategy including the following:

1). Adjust harvesting plans to include a mixture of age classes and forest types in some kind of landscape mosaic, and to increase connectivity between forest fragments. Although the mean number of taxa and their standardized abundance did not significantly differ between old and mature stands (Table 4-3), species diversity and trophic structure changed considerably with stand age (Tables 4-4 and 4-5; Figure 4-1). Harvesting, however, tended to increase species diversity and abundance (Table 4-3, Figure 4-1). In addition, many species were restricted to either forested or harvested stands or to one stand age (Tables 4-1 and 4-2). These data are similar to work on the saproxylic beetle fauna of Scots pine and Norway spruce in Europe, where diversity and abundance increased in managed forests, but the proportion of rare species was higher in primeval (=250 years) forests (Väisänen et al., 1993). It has been suggested that poor dispersal abilities of forest specialists and climatic factors between forest and harvested stands influenced the distribution of the fauna (Väisänen et al., 1993). Therefore, maximizing stand heterogeneity and connectivity should allow adequate movement of forest specialists between fragments.

2). During harvest, leave existing snags and logs in cutblocks. The similarity of the beetle fauna between old forest and 'old' harvested stands suggests that saproxylic faunas can survive forest harvesting for at least two years (Figure 4-2A). These harvested stands contained large volumes of CWM after harvesting, similar to what is found after wildfire. Siitonen and Martikainen (1994) have also suggested that the continuity of large, dead aspen across the landscape has a beneficial effect on saproxylic faunas. Therefore, CWM left in harvested stands may act as a sink for saproxylic species that are then able to recolonize the regenerating forest.

3). Leaving patches of individual and clumps of live trees in cutblocks, that become snags in the regenerating forest, may also help conserve saproxylic assemblages. It is unknown how long saproxylic insect assemblages remain intact after harvesting. If suitable host material becomes available during stand succession, maybe these assemblages can remain several years after harvesting. Only long term chronosequence studies can answer these questions.

The current paradigm in forest management is the 'natural disturbance model', which suggests that patterns of forest harvest should mimic the effects of wildfire on the landscape (Hansen et al., 1991; Probst and Crow, 1991; Hunter, 1993). Whether the succession of saproxylic invertebrates in burned and harvested stands is similar is unknown at present. Current research in chronosequences of harvested and burned aspen-mixedwood forests may elucidate these relationships.

Table 4-1. Relative standardized abundance of saproxylic beetle species collected from *Populus* coarse woody material of three decay classes (1-3), in old and mature boreal-mixedwood stands and recently harvested stands at Lac la Biche, Alberta from 1995. Insects were collected by passive window-traps attached to the boles of snags. Catches from window-traps are standardized to 1000 trap days. (^{a}P=predator, F=fungivore, WB=wood borer, S=scavenger, ?=unknown; ^{b}decay class; + denotes 1-10 individuals, ++ denotes 11-100 individuals, +++ denotes 101-500 individuals, ++++ denotes >500 individuals)

			Relative Standardized Abundance											
			Forest Stands						Harvested Stands					
			MATURE			OLD			MATURE			OLD		
Family	Species	Trophic Role^a	1^b	2	3	1	2	3	1	2	3	1	2	3
Anobiidae	*Hemicoelus carinatus* (Say)	WB	+++	++	++	+++	++	++	+	++	++	++	++	+++
	Ptilinus lobatus Casey	WB	+++	+			++	++	+++	+++	+++	+++	++	+++
	Tricorynus densus (Fall)	WB	+	++	++	++	++	+++	+	++	++	++	++	++
Anthribidae	*Allandrus populi* Pierce	F							+	++	++	++	+	++
	Tropideres dorsalis (Thunberg)	F								+	+			
Bostrichidae	*Endecatomus rugosus* (Randall)	WB				+		+						++
Buprestidae	*Agrilus liragus* Bart. and Brn.	WB							+++	+++	+++	++	+	++
	Dicerca tenebrica (Kirby)	WB							+++	+++	++++	+++	++	+++
Cantharidae	*Podabrus* spp.	P		+	+	+		+			+	+	++	++
Carabidae	*Agonum piceolum* (LeConte)	P							+					
	Agonum retractum LeConte	P									++			+
	Agonum sordens Kirby	P	+		+			+		+	+			
	Amara apricaria Paykull	P										+		
	Amara idahoana (Casey)	P									++			
	Bembidion spp.	P									++			
	Bradycellus lecontei Csiki	P							+					
	Calathus ingratus Dejean	P	++	+	++	++		+	++	++	++	++		++
	Calosoma frigidum Kirby	P	+++	++	++	+++	+++	++	++	++	+++	++		++
	Dromius piceus Dejean	P								+				
	Platynus decentis (Say)	P	+++	+++	+++	+++	+++	+++	+++	+++	++++	+++	+++	+++
	Pterostichus adstrictus Escholtz	P		+					++	++	+			++
	Pterostichus pensylvanicus LeConte	P		+					++	+	++	+		
	Pterostichus punctatisimus (Randall)	P						+						
	Stenolophus conjunctus (Say)	P										+		
	Syntomus americana Dejean	P								+	+			+
	Trichocellus cognatus (Gyllenhal)	P												++
Cephaloidae	*Cephaloon tenuicorne* LeConte	WB	+	++			+							
Cerambycidae	*Clytus ruricola* (Olivier)	WB							+++		+++			

	Grammoptera subargentata (Kirby)	WB	++	+	+		++			+		++		++
	Hyperplatys aspersa (Say)	WB								+	+			
	Judolia montivagens (Couper)	WB							++		++			
	Trachysida mutabilis (Newman)	WB	+++	++	++	++	++			++	++		++	+
Cerylonidae	*Cerylon castaneum* Say	F	++	++	++	++	+++	++		++	+++	++	++	++
Ciidae	*Cis americanus* Mannerheim	F								+				
	Cis levettei (Casey)	F				+		+	+		+			
	Dolichocis manitoba Dury	F				++		++				+		+
	Orthocis punctatus (Mellie)	F						+	++			+	+	
	Sulcacis curtula (Casey)	F								+	+			
Clambidae	*Clambus pubescens* Redtenbacher	F										++		+
Coccinellidae	*Psyllobora vigintimaculata* (Say)	F	+				+							
	Scymnus spp.	P										+		
Corylophidae	*Molamba biguttata* LeConte	F	++	++	++	+++	++	+	++++	++++	++++	++++	+++	+++
	Orthoperus scutellaris (LeConte)	F				+		+	++++		++++	++		+
Cryptophagidae	*Atomaria (Anchicera) ephippiata* Zimmerman	F	++							+	+	+		
	Atomaria (Anchicera) spp.	F	+							+				++
	Antherophagus ochraceus Melsheimer	F										++		
	Atomaria (Atomaria) spp.	F							++	++	++	++	+	+
	Caenoscelis spp.	F	+		++		+		+			++	+	+
	Cryptophagus acutangulus Gyllenhal	F												+
	Cryptophagus tuberculosis Maklin	F	++		++	+	+	++	+			+		++
	Henoticus spp.	F		+		++		++	+	++	++	++	+	++
Cucujidae	*Cucujus clavipes* Fab.	P	++	+		++	++	++		++	++	++	+	++
	Laemophloeus biguttatus (Say)	P												+
	Pediacus fuscus Erichson	P							++	++	+++	++	++	+++
Curculionidae	*Cossonus pacificus* Van Dyke	WB	++	+	+	+++	++	++		++	++	+++	++	+++
	Cryptorhynchus lapathi (L.)	WB							+		+			
	Phloeophagus canadensis Van Dyke	WB										+		
	Rhyncolus brunneus Mannerheim	WB												+
Dermestidae	*Dermestes lardarius* L.	S									++	+	++	+++
	Trogoderma sinistrum Fall	S				++		++			++	+	+	++
Elateridae	*Ampedus apicatus* (Say)	P					++	++	++	+++	+++	+++	++	+++
	Ampedus deletus (LeConte)	S	+	+	++	+	++	+	++	++	+++	+++		++
	Ampedus luctuosis (LeConte)	S	++					+	++	++	++	++	+	++
	Ampedus mixtus (Herbst)	S												+
	Ctenicera aeripennis (Kirby)	S										+		++
	Ctenicera resplendens (Escholtz)	S	++	+		++		++	++	+++	+++	++		++
	Megapenthes stigmosus (LeConte)	S	+									++	+	

Endomychidae	*Lycoperdina ferruginea* LeConte	F						+						
Erotylidae	*Dacne californica* (Horn)	F		+					++		++		+	
	Triplax californica LeConte	F	+++	++++	++	++	++	++	+++	+++	+++	+++	+++	+++
Eucinetidae	*Eucinetus punctulatus* LeConte	F					+	+		+	++			++
Eucnemidae	*Dirhagus pectinatus* (LeConte)	?										+		
	Epiphanis cornutus (Escholtz)	?	+		+	+		+						
	Hylis terminalis (LeConte)	?	+		+									
Histeridae	*Abraeus bolteri* LeConte	P												++
	Platysoma lecontei Marseul	P							++	++	++	++		++
	Teretrius montanus Horn	P	+			++	+	++	+	++	++	++	++	+++
Hydrophilidae	*Cercyon cinctus* Smetana	S	+								++	+		+
	Cercyon pygmaeus (Illiger)	S			+					++	++			
Lampyridae	*Ellychnia corrusca* (L.)	P		+								+		
	Pyractomena borealis (Randall)	P									++	+		++
Lathridiidae	*Cartodere constricta* (Gyllenhal)	F	++		++				++	++	++	++		+
	Corticaria sp A	F	+	+	++	++	++	++			++	++	++	++
	Corticaria sp B	F	++		++		+	+		+	++			++
	Corticaria sp C	F				++	+	+	+	++	++	+	++	++
	Corticaria sp D	F				+		+						
	Corticaria sp E	F	+		++			++	++		++	++	+	++
	Corticaria sp F	F							++++		++++			
	Corticarina spp.	F							+			++		
	Cortinicara gibbosa (Herbst)	F				+								+
	Enicmus sp A	F				++	+	++	+	++	+	++		++
	Enicmus sp B	F									++	+		+
	Enicmus sp C	F	++						++		++			
	Lathridius sp A	F	++	++	++	+	++	+	++	++	+++	++	+	++
	Lathridius sp B	F	++		+			+	++	++	++	++	++	++
	Melanopthalma pumilla (LeConte)	F	++++	++++	+++	+++	+++	+++	++++	++++	++++	++++	+++	+++
	Melanopthalma villosa (Zimmerman)	F	++++	+++	++++	+++	+++	+++	+++	++++	++++	+++	+++	+++
Leiodidae	*Agathidium* spp.	F	++		++	+++	++	++	++	++	+++	+++	++	+++
	Anisotoma spp.	F												+
	Catops americana Hatch	S	+											
	Hydnobius spp	F										+		
	Leiodes spp	F								+	+			
Lyctidae	*Lyctus planicollis* LeConte	WB	++	++	+	+++	++	++	++	++	++	++	++	++
Lymexylidae	*Hylecoetus lugubris* Say	WB	+			++		++				++		
Melandryidae	*Dircaea liturata* (LeConte)	?	++									++		
	Enchodes sericea (Haldeman)	?	++		++	+	++	+				++		+

	Melandrya striata Say	?	+++	++	+	+++	++	++	++	++	++	++	++	++
	Orchesia castanea (Melsheimer)	F		+		+		+				++		+
	Phryganophilus collaris LeConte	?						+						
	Zilora hispida LeConte	?	+			+	++	+		++	++	++		++
Mycetophagidae	*Mycetophagus distinctus* Hatch	F		+		+	+			+	++	++		++
	Mycetophagus pluripunctatus LeConte	F		++		++			+		++			+
Nitidulidae	*Epuraea* spp.	F	++	++		++++	++	+	+++	+++	++++	++++	++	++
	Glischrochilus moratus Brown	F				++			++	+	++	++	++	++
	Glischrochilus sanguinolentus (Olivier)	F				+			++		++			
	Glischrochilus siepmanni Brown	F	++		+	+++			++	+++	+++	+++		
	Glischrochilus vittatus (Say)	F							++		++			
Pselaphidae	*Batrisodes* spp.	P										++		
	Euplectus duryi Casey	P						++	+	++	++	++		
Ptiliidae	*Acrotrichus* spp.	F	++		+			+	+	+	++	+		
Pyrochroidae	*Dendroides testaceus* LeConte	F	++	++	++	+	++		++	++	+++	++	+	+
Rhipiphoridae	*Pelecotoma flavipes* Melsheimer	?		+					+	+	++			+++
Rhizophagidae	*Monotoma picipes* Herbst	F							+					
	Rhizophagus dimidiatus Mannerheim	P							++		++			
	Rhizophagus bruneus Horn	P	++		+	++++	+++	++	++	++	++	++++	++	++++
	Rhizophagus remotus LeConte	P	++			+++	++	++	++	+++	+++	++++	++	+++
Salpingidae	*Sphaeriestes virescens* (LeConte)	P							++	++	+++	+	++	++
Scolytidae	*Procryphalus mucronatus* (LeConte)	WB							++		+++	+++	+	++
	Trypodendron retusum (LeConte)	WB				+++			+	+	+++	++++		+
Scraptiidae	*Anaspis rufa* Say	?							++	+	++			
	Canifa pallipes (Melsheimer)	?	+	+		++	++	++	++	+++	+++	++	++	+++
Sphindidae	*Sphindus americanus* LeConte	F		+		+	++	+		+				+
Staphylinidae	*Acidota crenata* (Fab.)	P							+	+				+
	Aleocharinae	?	++	++	++	+++	++	++	+++	+++	++++	+++	++	+++
	Bolitobius horni Campbell	P												+
	Bryophacis smetanai Campbell	P				+		+		+	+			
	Carphacis nepigonensis (Bernhauer)	P	++	++		++++	++	++	+++	+++	+++	++++	++	+++
	Coproporus ventriculus (Say)	S												+
	Lordithon bimaculatus (Couper)	P				+++				+	+	++		++
	Lordithon fungicola Campbell	P				++	+	++		+	++	+		++
	Megarthrus sinuacticollis Bois. and Lac.	?									++			
	Mycetoporus fimbriatum Campbell	P									++			
	Mycetoporus splendidus (Gravenhorst)	P										++		
	Nudobius cephalus (Say)	P							++	++	++	++		+
	Olisthaerus megacephalus (Zetterstedt)	P				+	+				++	++		

	Philonthus cyanipennis (Fab.)	P				++	+	++						
	Pycnoglypta campbelli Gusarov	P										++		
	Quedius plagiatus Mannerheim	P	+			++				++	+	++	+	++
	Quedius rusticus Smetana	P											++	
	Siagonum punctatum LeConte	S				+		+				+	+	
	Staphylinus pleuralis LeConte	P										+		
	Tachinus basalis Erichson	P				+					++			
	Tachinus elongatus Gyllenhal	P	++	+										
	Tachinus fumipennis (Say)	P												+
	Tachyporus abdominalis (Fab.)	P							+		+			
	Tachyporus maculicollis LeConte	P									+			
	Tachyporus nimbicola Campbell	P												+
Tenebrionidae	*Bius estriatus* (LeConte)	F										+		++
	Mycetochara fraterna (Say)	F	++	++		++	++					+	+	+
	Platydema americanum Cast.and Brul.	F				+		+						+
	Scaphidema aeneolum (LeConte)	F	+		+									+
	Upis ceramboides (L.)	F				++	++	++				+		+
Trogossitidae	*Tenebroides mauritanicus* Chevrolet	P		+								++		++
	Thymalus marginicollis (L.)	P	++	++			++	+	+	+	++			+

Table 4-2. Number and characterization of saproxylic species caught only in a single stand type. The number of rare species included among unique species is given in parentheses. Species were categorized as rare if fewer than 10 individuals per 1000 trap days were captured. Families and trophic roles from Table 4-1. ([a]F=fungivore, P=predator, WB=wood borer, S=scavenger; ?=unknown)

Stand type	**Unique species**	**Families**	**Trophic roles[a]**
Old Forests	6(1)	Carabidae(1); Melandryidae(1); Staphylinidae(4)	P(5); ?(1)
Mature Forests	3(1)	Eucnemidae(1); Leiodidae(1); Staphylinidae(1)	P(1); S(1); ?(1)
Old-Harvest	25(15)	Carabidae(3); Clambidae(1); Coccinellidae(1); Cryptophagidae(2); Curculionidae(2); Elateridae(1); Eucnemidae(1); Histeridae(1); Leiodidae(2); Pselaphidae(1); Staphylinidae(8); Tenebrionidae(1)	F(6); P(13); WB(2); S(2); ?(1)
Mature-Harvest	22(7)	Anthribidae(1); Carabidae(5); Cerambycidae(3); Ciidae(2); Curculionidae(1); Lathridiidae(1); Leiodidae(1); Nitidulidae(1); Rhizophagidae(2); Scraptiidae(1); Staphylinidae(4)	F(7); P(9); WB(4); ?(2)

Table 4-3. Mean (±standard error) number of families, genera, species, and standardized abundance, per sample, of saproxylic beetles collected with window-traps attached to snags of three decay classes in old and mature aspen-mixedwood stands and recently harvested stands near Lac la Biche, Alberta in 1995. See Appendix 7 for analysis of variance.

	Old stands	Mature stands	Forest stands	Harvested stands	Decay class1	Decay class 2	Decay class 3
Number of Families	17.9±1.10	14.7±1.05	12.3±1.05	20.5±1.10	16.6±0.89	15.6±0.96	16.5±0.89
Number of Genera	26.4±1.73	21.5±1.65	16.9±1.65	31.3±1.73	25.4±1.67	21.3±1.79	24.5±1.67
Number of Species	29.1±1.96	23.6±1.88	18.5±1.88	34.7±1.96	27.8±1.71	23.2±1.83	27.3±1.71
Abundance	1045.3±122.24	878.5±117.04	552.9±117.04	1400.5±122.24	1301.4±98.80	727.1±105.67	817.5±98.80

Table 4-4. Shannon-Wiener (H') and Berger-Parker (1/d') diversity indices based on saproxylic Coleoptera collected with window-traps attached to *Populus* snags of three decay classes in old and mature boreal mixedwood stand and recently harvested stands near Lac la Biche Alberta, 1995. Index calculations are based on pooled samples from each sample unit. See text for explanation of indices.

Sample Unit	**Shannon-Wiener H'**	**Berger-Parker (1/d')**
Old forest stands	3.45	8.19
Mature forest stands	2.96	4.85
Old stand harvested	3.65	9.00
Mature stand harvested	3.35	5.21
Decay class 1-old forest stands	2.99	5.05
Decay class 2-old forest stands	3.36	7.93
Decay class 3-old forest stands	3.37	6.45
Decay class 1-mature forest stands	3.09	5.85
Decay class 2-mature forest stands	2.52	3.62
Decay class 3-mature forest stands	2.66	4.14
Decay class 1-old stand harvested	3.28	7.19
Decay class 2-old stand harvested	3.34	7.57
Decay class 3-old stand harvested	3.83	13.69
Decay class 1-mature stand harvested	3.07	5.61
Decay class 2-mature stand harvested	3.25	4.97
Decay class 3-mature stand harvested	3.14	5.00

Table 4-5. Mean (±standard error) absolute and proportional abundance of fungivores, predators, wood borers, scavengers and unknown roles, per sample, of saproxylic beetles collected with window-traps attached to snags of three decay classes in old and mature aspen-mixedwood stands and recently harvested stands near Lac la Biche, Alberta in 1995. See Appendices 8 and 9 for analyses of variance.

	Old stands	Mature stands	Forest stands	Harvested stands	Decay class1	Decay class 2	Decay class 3
Absolute abundance							
Fungivores	397.93±42.62	556.15±40.80	269.77±40.80	710.35±42.62	616.17±49.89	422.33±53.34	395.67±49.89
Predators	390.51±89.43	147.82±85.62	171.50±85.62	364.67±89.43	418.13±59.27	154.46±63.36	205.39±59.27
Wood Borers	164.52±16.11	87.11±15.42	68.60±15.42	184.72±16.11	171.09±26.07	76.07±27.88	119.23±26.07
Scavengers	26.13±6.29	28.58±6.02	7.35±6.02	49.29±6.29	24.91±5.35	18.66±5.73	37.56±5.35
Unknown	66.22±4.93	58.80±4.72	35.66±4.72	91.46±4.93	71.05±7.23	55.53±7.73	59.62±7.23
Proportional abundance (%)							
Fungivores	40.4±3.18	63.6±2.61	53.2±2.61	51.8±3.18	47.9±3.14	58.4±3.36	51.9±3.14
Predators	33.5±3.66	17.8±3.30	26.2±3.30	24.4±3.66	30.1±1.92	21.6±2.06	23.7±1.92
Wood Borers	16.3±0.89	9.4±0.85	12.2±0.85	13.2±0.89	13.2±1.76	10.8±1.88	13.9±1.76
Scavengers	2.2±0.41	2.7±0.39	1.4±0.39	3.6±0.41	1.8±0.33	1.9±0.35	3.7±0.33
Unknown	7.5±0.82	6.6±0.79	7.1±0.79	6.9±0.82	6.9±1.03	7.4±1.10	6.8±3.91

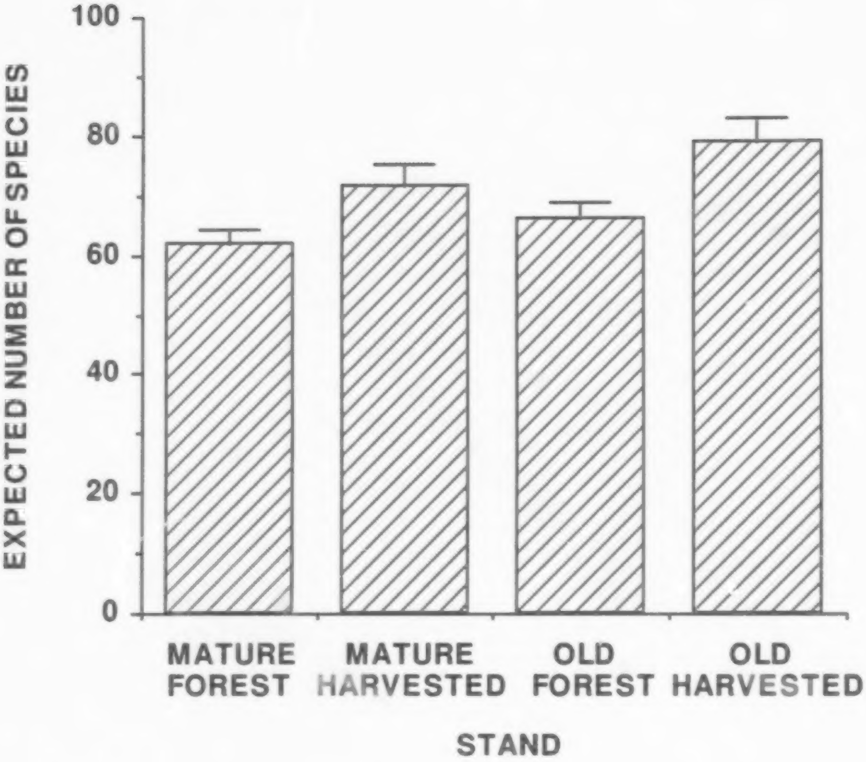

Figure 4-1. Rarefaction estimate (mean ± standard deviation) of saproxylic beetle species richness from window-traps on snags in forest and harvested stands near Lac la Biche, 1995. Species estimates are based on a subsample size of 550 individuals.

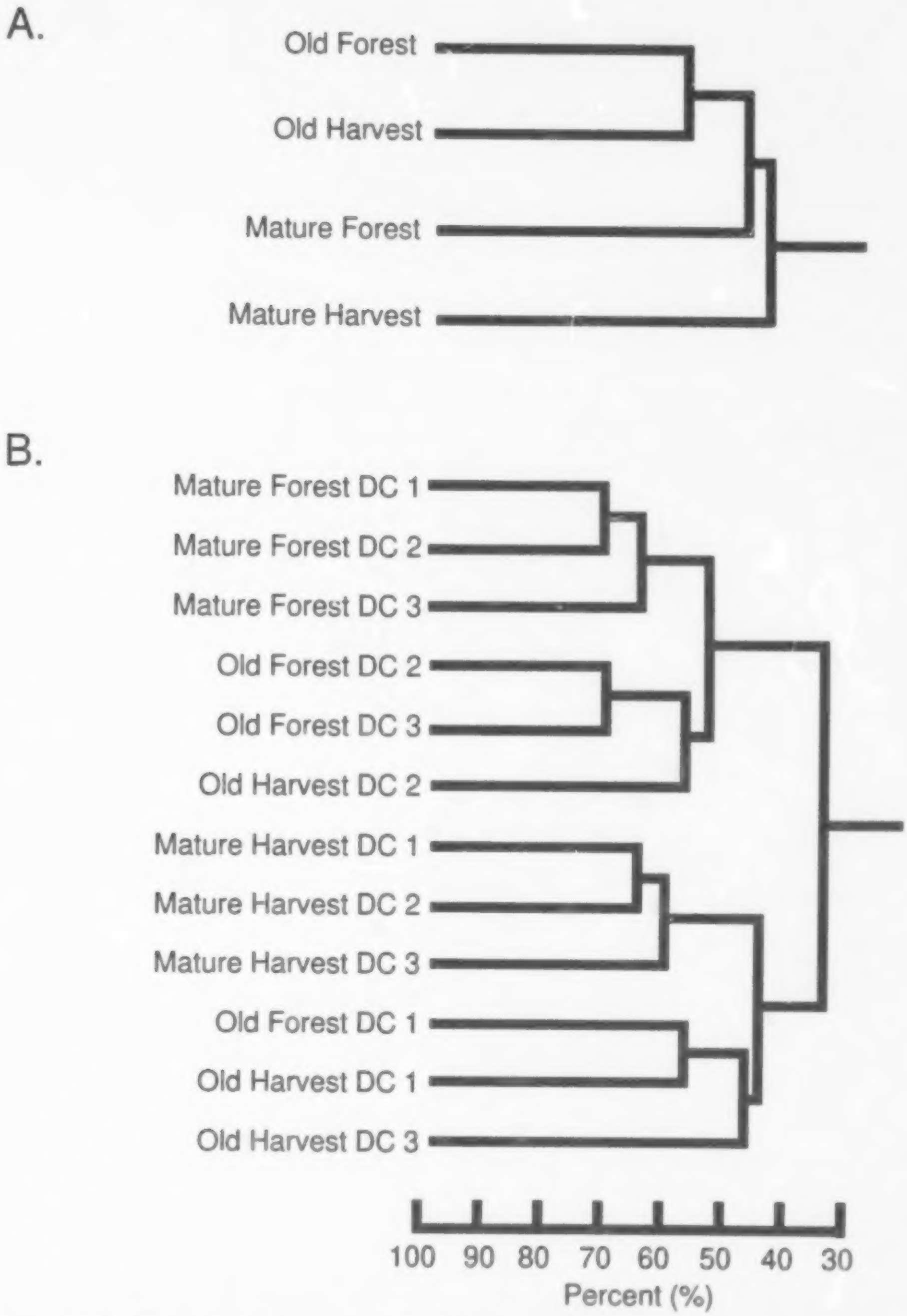

Figure 4-2. Bray-Curtis percent similarity of the saproxylic beetle fauna sampled by window-traps on snags, near Lac la Biche, 1995, between; A. forested and harvested stands, B. decay classes in forest and harvested stands.

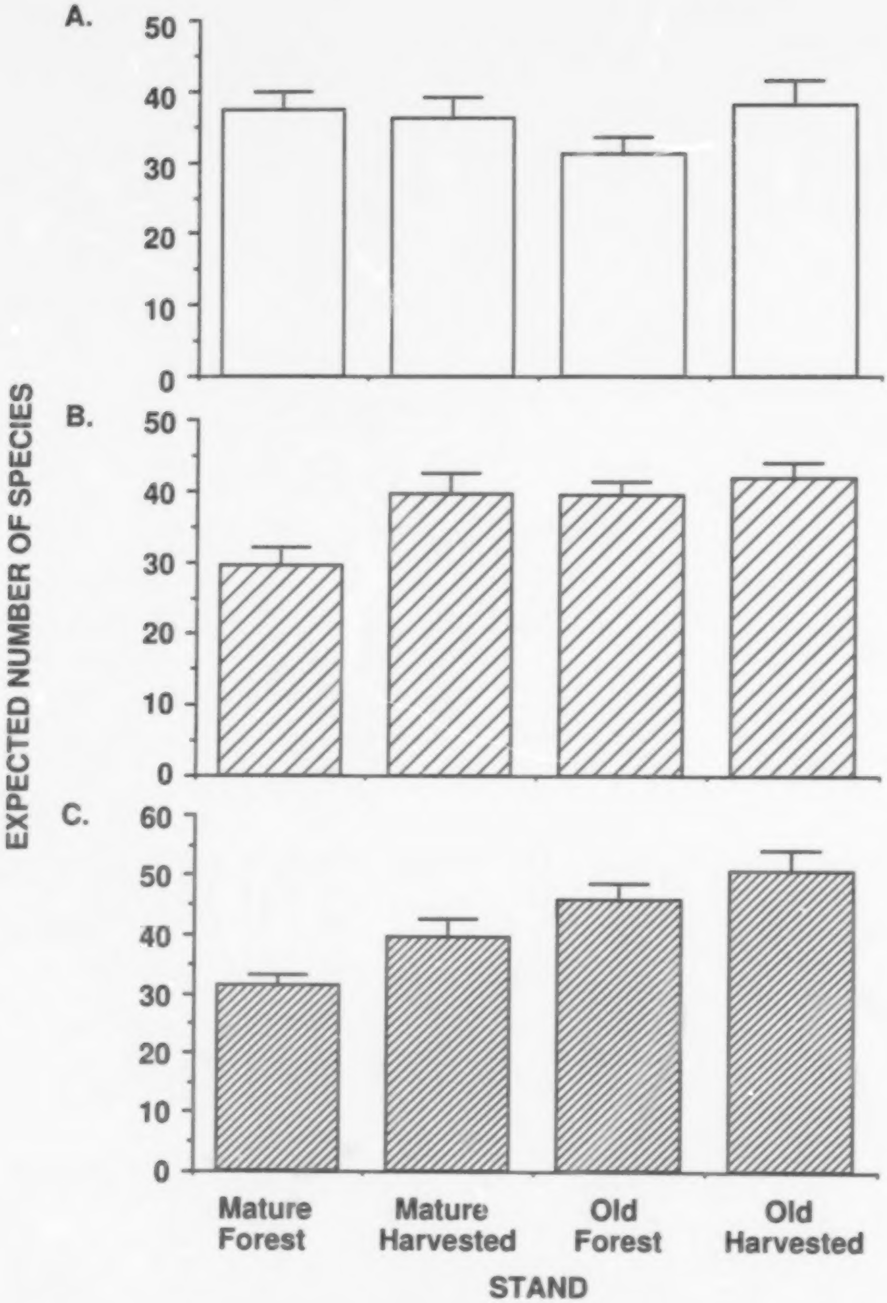

Figure 4-3. Rarefaction (mean±1 standard dev.) estimates of saproxylic beetles species richness from forest and harvested stands near Lac la Biche in 1995, A. decay class 1, B. decay class 2, C. decay class 3.

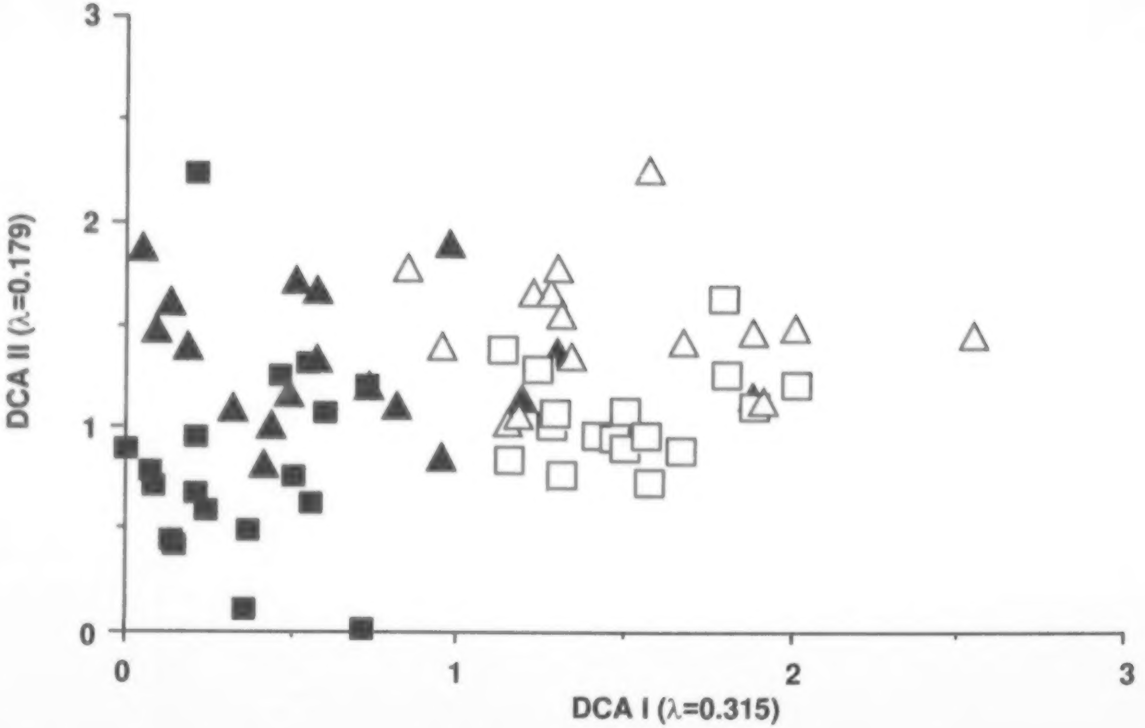

Figure 4-4. Detrended correspondence analysis (DCA) of the saproxylic beetle fauna collected with window-traps near Lac la Biche, 1995. The first DCA axis relates to factors associated with stand type (i.e. forest versus harvest), and the second axis relates to factors associated with stand age.
(Mature forest stands ■, Old forest stands ▲, harvested mature stands □, and harvested old stands △)

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5. The Early Colonization of *Populus* Coarse Woody Material by Arthropods and Their Influence on Decay Rate

5.1 Synopsis

The colonization of newly created coarse woody material (CWM) by arthropods and their effect on wood decay rate was studied at two sites in the aspen-mixedwood forest in Alberta. New dead woody material was created in 1993 by cutting 'healthy' trees into three sections, a stump section, a snag section, and a log section. Insects were then reared from wood samples from each section in 1994 and 1995 to determine the temporal sequence and mode of wood colonization. This fauna is rather dynamic as shown by the large change in faunal composition across two years. The dominant arthropod groups reared from new CWM include the Acari, Collembola, Psocoptera, Diptera and Coleoptera. There were three very abundant beetles in new CWM, *Trypodendron retusum* (LeConte), an ambrosia beetle, its major predator *Rhizophagus remotus* LeConte, and *Molamba biguttata* (LeConte), a fungivore. Two other beetles, *Endomychus biguttata* Say, and *Megatoma cylindrica* Kirby, appear to specialize on new dead wood. The number of species, genera, families and abundance, as well as wood borer activity, appeared higher in 1994 than in 1995. Old forest stands tended to have higher taxon richness compared to mature stands. In addition, wood borers tended to form a higher proportion of the fauna from 'snags'; whereas, predators tended to form a higher proportion of the fauna from logs and stumps, suggesting that host-finding and dispersal capabilities may be very important for this fauna. Significant changes in wood hardness (*i.e.* a measure of wood decay) could not be detected in the first two years after a tree dies. These data suggest that the arthropod fauna attracted to new dead wood have a minor role in speeding up decay initially, but likely affect wood decomposition in the long term.

5.2 Background and objectives

A large percentage of biomass in boreal aspen-mixedwood forests is made up of sub-merchantable timber and coarse woody material (CWM). In fact, it has been estimated that healthy aspen forest stands contain between 10-20 Mg ha^{-1} (Harmon et al., 1986), or up to 29% of above and below ground biomass, as snags, logs, stumps, and other forms of dead woody material (Peterson and Peterson, 1992). Dead and dying woody material has many important structural roles in forest ecosystems, including habitat for autotrophs and heterotrophs, and regulation of geomorphic processes such as soil erosion and the downslope movement of water and litter (Harmon et al, 1986). Dead wood is also important in nutrient dynamics as it contributes significant amounts of nitrogen, carbon, phosphorus, potassium, calcium, magnesium and other nutrients to forest soils (Ausmus, 1977; Swift, 1977; Hendrickson, 1988; Hendrickson et al., 1989). Woody material decomposes rather slowly and is low in nutrient quality compared to needles and foliage, but is a significant long-term source of nutrients (Larsen et al., 1978; Vogt et al., 1986; Alban and Pastor, 1993; Kauffman et al., 1993). Nitrogen, a nutrient shown to be limiting in forest ecosystems, is often abundant in CWM (Harmon et al., 1986; Hendrickson, 1988; Hendrickson et al., 1989).

Regulation of CWM decomposition is influenced by the invertebrate fauna associated with this resource (Ausmus, 1977; Swift, 1977). Generally, wood boring beetles are the first to colonize weakened or newly dead trees, and are attracted to them by volatiles such as ethanols and terpenes given off by the tree (Roling and Kearby, 1975; Millar et al., 1986; Witcosky et al., 1987; Ytsma, 1989; Schroeder, 1992). Also, symbiotic relationships between some beetle species and fungi have also developed which increase the ability of these organisms to colonize and utilize woody material. The best known examples include bark and ambrosia beetles and their associated ambrosia and stain fungi (e.g. Chapman, 1966; Abrahamson et al., 1967; French and Roeper, 1972; Wood, 1982; Brewer et al., 1988). Some beetles gain nutrients directly from fungi (e.g. ambrosia beetles and ambrosia fungi), but many other beetle species are simply vectors of decay fungi. The close association between insects and decay fungi thus has an important influence on the rate of decay in wood (Gardiner, 1957; Wallis et al., 1971; Zhong and Schowalter, 1989; Lowell et al., 1992).

Recent work on the arthropod fauna associated with *Populus* CWM has shown that the fauna is large, diverse, and sensitive to spatial scale (see Chapters 2 and 3). Given the important roles that this fauna plays in forest ecosystems, and its sensitivity to forest harvesting (see Chapters 3 and 4; Heliövaara and Väisänen, 1984; Väisänen et al., 1994; Siitonen and Martikainen, 1994), a better understanding of the structure and function of this fauna in mixedwood ecosystems can contribute to evolving forest management strategies, which aim to minimize harvesting impacts on ecosystem integrity.

The objectives of this chapter were to investigate the early colonization of CWM by arthropods, and to assess the influence of these organisms on the initiation and rate of wood decay. I tested the hypothesis that wood colonized by arthropods decomposes at a faster rate than wood without arthropods. The Coleoptera were the focus of the inventory portion of this work because: it is one of the dominant insect orders in CWM (see Chapters 2 and 4, Speight, 1989); the taxonomy of many beetle families is relatively well known; the distribution of beetles in Canada is well known, and has been recently documented in a checklist of species published by Bousquet (1991); this order is diverse with respect to species and trophic role; Coleoptera are easy to collect, preserve and store for later identification; and it facilitates comparisons with most previous studies of the CWM fauna, which focused on beetles (e.g. Fager, 1968; Speight, 1989; Väisänen et al., 1993; Käila et al., 1994; Jonsell and Nordlander, 1995).

5.3 Methods

5.3.1 Stand descriptions and experimental design

New CWM was created in May and early June of 1993 to investigate the colonization of new dead wood by insects and fungi, and to determine their effects on wood decay rate. The experiment was set up in two regions in northern Alberta, in the Lac la Biche area, near Touchwood Lake (54° 51' N, 111° 27' W), and in the Fairview area, near Eureka River (56° 35' N, 118° 37' W). These study sites are aspen dominated stands (<20% conifer canopy and understory trees), but also include a mixture of balsam poplar, white spruce (*Picea glauca* [Moench] Voss) and birch (*Betula* spp.). Stand structure was described in detail in Chapters 2 and 3.

Increment core samples, extracted at breast height from the heartwood of standing live trees, were used to determine the amount of fungal infection. Trees with minimal infection (i.e. with less than 20% fungal stain of the core sample) were then chosen for this experiment. In each replicate four aspen or poplar trees, representative of the dominant size class of each stand, were cut to create new CWM. Each tree was cut so as to leave a 120 cm-high stump in the ground, to sample insects entering the wood through the root system or by walking. An additional two 120 cm-long sections were cut from the base of each felled tree. One was left on the ground to serve as a log, to sample insects colonizing the wood by walking; and the second was suspended with rope and chain from a beam lashed between two trees and served as a 'snag', to sample insects colonizing the wood by flight. The lower end of snag sections were 1.0-2.0 m above the ground. The remainder of each felled tree was left in place and was not used in the experiment. Exposed areas of all cut sections were sealed with paraffin to slow moisture loss from the wood. All three sections of one of the four trees was covered with insect screen to prevent infestation by insects; the stump could only be screened to exclude flying insects. The experiment was replicated in three old (>100 years) and three mature (40-80 years) stands near Lac la Biche and two old and two mature stands near Eureka River. All sites were visited every 2-3 weeks from May to September and damage to insect screening repaired.

In early spring of 1994 a 60 cm wood bolt was cut from each snag, log and stump section from each stand and transported back to the lab. The newly cut exposed face of each wood section remaining in the field was then re-sealed with paraffin, and screen replaced on previously screened sections. Sections were labeled and placed in plastic bags to prevent insects escaping, and then transported to Edmonton. In Edmonton, the ends of each wood section were sealed with paraffin to slow moisture loss, and each section placed in a sealed cardboard box. Each box had a 3 cm diameter hole cut in the bottom and a clear plastic container (4 cm diameter) was glued to the box by means of a lid with a 3 cm hole cut into it. The container thus functioned as a pitfall trap. Insects which emerged from the wood were attracted to the light shining through the plastic container and would be collected. Boxes were checked weekly from mid May to mid October, 1994. The wood sections remaining in the field were similarly collected and reared in 1995.

The amount of wood decay of each wood bolt was measured using an h-gun, an experimental prototype developed by researchers at the

Northern Forestry Center (Natural Resources Canada). The h-gun (Figure 5-1) tests the hardness of wood by measuring the amount of force needed to inject a 6 cm needle into the wood. An increasing hardness measure is inversely related to the amount of decay. Three hardness measurements were made on each snag, log and stump section, one from the center of each end, and one through the bark on the side of each section.

5.3.2 Data analyses

Only saproxylic beetle species were included in the analyses, and are listed in Table 5-1. Because wood volume and the number of rearing days was not the same for all samples, catches from rearings were standardized to 0.1 m^3 of wood and 150 rearing days.

Mean number of taxa and mean standardized abundance were calculated using pooled data from all three unscreened logs, snags or stumps from each replicate. Pooled estimates were analyzed using a 5-way analysis of variance (ANOVA; GLM), in a split plot design, in SAS. The main effects in this analysis were region, stand age, treatment (i.e., screened or unscreened wood section), wood section (i.e., log, snag, or stump), and year of rearing. Trophic composition from wood sections was also studied using a similar design. Beetle taxa were assigned one of four trophic roles, predator, fungivore, wood borer, and scavenger, based on the biology of the predominant life stage found in dead wood. If the trophic role of a species was uncertain, it was assigned to an 'unknown' category. The standardized proportion of each trophic role was calculated from data pooled across all three unscreened log, snag and stump sections from each replicate. The catches from the pooled experimental sections and each control section, were also analyzed using ANOVA (GLM) in SAS.

The three wood hardness measurements for each wood section were averaged, and mean wood hardness values were then tested using ANOVA (GLM) in SAS. Full ANOVA tables for each of the three analyses stated above are presented in Appendices 10-12.

5.4 Results

A total of 6948 arthropods were reared from CWM sections, of which 2381 were collected in 1994 and 4567 collected in 1995. In 1994, Coleoptera (beetles) and Diptera (flies) were the two dominant groups reared from one-year-old wood sections, making up approximately 36%

and 38% of the total catch, respectively (Figure 5-2A). In 1995, the dominant group reared from two-year-old wood sections was the Diptera, making up 50% of the total catch (Figure 5-2A). Acari (mites) increased from 5% of the catch in 1994 to 27% of the catch in 1995 (Figure 5-2A). Beetle abundance dropped markedly to only 7% of the total catch in the second year, and Psocoptera (bark lice) abundance dropped from 12% in 1994 to 3% in 1995. Four orders, the Hemiptera (true bugs), Homoptera (hoppers, aphids, etc.), Thysanoptera (thrips), and the Trichoptera (caddisflies) showed overall abundance of less than one percent (Figure 5-2B).

Beetle species and their standardized abundance collected by wood section and year is shown in Table 5-1. A total of 900 beetles, comprising 35 species were collected from wood in 1994, with abundance dropping to 293 individuals from 43 species collected in 1995. The most abundant Coleoptera taxa were an ambrosia beetle, *Trypodendron retusum* (LeConte), a minute fungus beetle, *Molamba biguttata* (LeConte), and a predaceous beetle thought to feed on scolytid larvae, *Rhizophagus remotus* LeConte, which together comprised approximately 70% of the total catch. Interestingly, all of the *T. retusum* specimens were collected in the first year. Also, four beetle species were collected from recently killed wood that were not collected in other decay classes (see Chapters 3 and 4), two ground beetle species *Agonum obsoletum* (Say) and *Psydrus piceus* LeConte, a fungus beetle *Endomychus biguttata* Say, and a dermestid *Megatoma cylindrica* (Kirby) (Table 5-1).

There were many significant differences between the mean number of beetle species, genera, families and abundance, according to parametric analysis. Although there were no effects of region or wood section in taxon richness and abundance (Table 5-2), taxon richness was significantly higher in old stands than mature stands for the mean number of species (df=1, F=9.71, P=0.0207), genera (df=1, F=8.08, P=0.0294), and families (df=1, F=9.69, P=0.0208) (Table 5-2). Unscreened wood sections had a significantly higher mean number of species (df=1, F=37.93, P=0.0001), genera (df=1, F=41.12, P=0.0001), families (df=1, F=46.60, P=0.0001), and standardized abundance (df=1, F=17.29, P=0.0002) than wood sections screened with insect mesh (Table 5-2). Also, collections made in 1994 had a significantly higher number of families (df=1, F=8.42, P=0.0273) and standardized abundance (df=1, F=15.52, P=0.0076) than collections in 1995 (Table 5-2). There were also significant interactions of year with: stand age for the number of genera (df=1, F=7.96, P=0.0303), families (df=1, F=6.31, P=0.0457), and standardized abundance (df=1, F=5.37, P=0.0597), with more taxa and individuals collected in 1994 (Table 5-3); treatment, with a significantly higher abundance collected from unscreened logs in 1994 (df=1, F=9.96, P=0.0031) (Table 5-3); and section, with a significantly higher number of species (df=2, F=4.55, P=0.0168), genera (df=2, F=5.11, P=0.0107), families (df=2, F=4.31, P=0.0204) and abundance (df=2, F=5.78, P=0.0063) from snags in 1994 (Table 5-3).

There were no significant main effects of proportional abundance for fungivores, scavengers and unknowns (Table 5-4). Predators were proportionally more abundant in old stands than in mature stands (df=1, F=6.39, P=0.0448), and in logs and stumps than in snags (df=2, F=9.82, P=0.0005) (Table 5-4); however, the significant section x age interaction indicates that the differences among sections is greater in old stands than in mature stands (df=2, F=4.06, P=0.0268) (Table 5-5). Wood borers were proportionately more abundant in unscreened sections (df=1, F=9.79, P=0.0037), in snags than in stumps and logs (df=2, F=5.41, P=0.0094), and in 1994 than in 1995 (df=1, F=18.00, P=0.0054) (Table 5-4); however, the significant year x region interaction indicates that the temporal differences were much greater in Lac la Biche than in Eureka River (df=1, F=9.01, P=0.0240) (Table 5-5).

Wood collected from Eureka River had significantly (df=1, F=49.52, P=0.0004) higher (16.2±0.8) mean hardness values than wood from Lac la Biche (8.5±0.7). No other significant differences in wood hardness were apparent.

5.5 Discussion

5.5.1 Early colonization of CWM

The dominant arthropod groups collected from newly created *Populus* CWM were similar to what was found from *Populus* in other decay classes (Chapter 2), in that Acari, Collembola, Psocoptera, Coleoptera and Diptera form the largest groups reared (Figure 5-2). The

Hymenoptera, of which the vast majority were ants and parasitoids, formed a large percentage of the groups from dead wood of all decay classes, but is under-represented in new CWM; whereas, the Psocoptera, which formed a small percentage of the taxa collected from all decay classes, is rather abundant in new CWM (Chapter 2, Figure 5-2). This may be directly related to the biology and habitat preferences of these two groups. Ants, such as *Camponotus* and *Formica* , are usually associated with 'soft' wood typical of later decay stages, and often gain access to the wood through holes and cracks in the bark (Ives and Wong, 1988). Psocids, on the other hand, are known to be primarily phytophagous, feeding on algae, lichens, foliage and molds on and beneath the bark surface, with some groups known to oviposit on tree branches and trunks (Imms, 1957; Borror et al., 1976). New CWM sections in this study had, for the most part, the bark still intact, and the wood still sound (see discussion below) and was therefore not suitable for ant colonization, but may have provided necessary food sources and oviposition sites for psocids.

The arthropod data also suggest that the fauna begins to develop in year two, after wood boring beetle abundance drops (Table 5-1; Figure 5-2). These data suggest that wood boring beetles may 'pre-condition' the wood for colonization by other arthropods. Beetle galleries may allow direct access to fungi and phloem resources, and increase the surface area available for colonization by other arthropods (Zhong and Schowalter, 1989). Groups such as Collembola, Acari, and Diptera, many of which are fungivorous, greatly increased in abundance in year two (Figure 5-2). Work by Howden and Vogt (1951) and Fager (1968) also showed that the abundance and diversity of arthropods entering CWM increased during, or just after, initial colonization by wood boring beetles. Unfortunately, much of the work focusing on wood decay has looked exclusively at the effects of wood boring pests and their symbiotic fungi (e.g., Wallis et al., 1971; Edmonds and Eglitis, 1989; Zhong and Schowalter, 1989; Lowell et al., 1992, Schowalter et al., 1992) and very little is known about the complex interactions of wood boring beetles and other arthropod taxa.

Although the proportion of Coleoptera collected from new CWM was similar to other decay classes (see Chapter 2), the beetle fauna was less diverse. Beetle rearings from decay class 1 wood, which is the most similar to CWM in this study, yielded an average of 12, 11 and 8 species, genera, and families, respectively, per rearing (see Chapter 3); whereas, only 2.5, 2.4 and 2.2 species, genera and families, respectively, were collected in rearings from new CWM. These differences are probably due to differences in wood volume reared and the surface area available for colonization; in a sense, the smaller the wood chunk the harder it is to find. In addition, smaller wood sections may also entirely lack certain microhabitats typical of larger wood sections (see Chapter 2), and hence, the fauna associated with these habitats is absent.

Weakened and newly dead wood has a unique fauna which is rare or absent in more decayed material. Many wood- and bark-boring beetles such as cerambycids, buprestids, and scolytids have a requirement for fresh host material in order to complete development (Wood, 1982; Brewer et al., 1989), and are therefore among the first insects to attack fresh CWM (Samuelsson et al., 1994). These insects are usually good dispersers, and have excellent host-finding capabilities mediated by long-range attraction to odors, such as ethanol and terpenes, emanating from weakened and newly dead trees (Chapman, 1963, 1966; Witcosky et al., 1987). In this study, the cambium feeding buprestid, *Agrilus liragus* (Bart. and Brn), and the ambrosia beetle, *Trypodendron retusum*, were abundant in 1-year-old CWM, and greatly decreased in abundance in 2-year-old wood (Table 5-1). In fact, the overall significant decrease in beetle abundance (Table 5-2) and wood borer abundance (Table 5-4) from 1994 to 1995 was due largely to the decrease in abundance of *T. retusum*. It may be that ambrosia fungi cultured in the galleries of this beetle, and eaten by its larvae, cannot compete with other fungi which eventually invades the wood (Boddy, 1992). Thus, this species is rarely found in more advanced decay classes, or when it is found, may simply be a collecting artifact.

Predaceous insects which specialize on bark- and wood-boring beetles also contributed to the faunal uniqueness of early colonizers. For example, the abundance of *Rhizophagus remotus* and *R. brunneus* Horn, specialist predators of *T. retusum* and other scolytids (Bousquet, 1990), reflects the presence and absence of its host.

Several fungivorous groups, including the Leiodidae, Cerylonidae, Cryptophagidae, and especially the Corylophidae, also seem to specialize in fresh CWM. The endomychid, *E. biguttata*, was collected only in recently dead wood (Table 5-1). This may indicate a preference for fungi present in *Populus* trees as they die or immediately after death. For example, fungi from the genera *Hypoxylon, Peniophora, Phellinus* and *Armillaria* are common in living and freshly killed *Populus* (Hiratsuka and Loman, 1984; Hiratsuka, 1987; Peterson and Peterson, 1992). Specialized fungivores may be attracted to odors emanating from these fungi (Hedlund et al., 1995; Jonsell and Nordlander, 1995), and gain access to the mycelial masses through holes made by *T. retusum*. These species may disappear from older CWM because of the absence of the appropriate food source or due to competition with other fungivorous species (Boddy, 1992). In fact, temporal changes in the arthropod fauna inhabiting CWM may be tightly linked to changes in fungal community structure over time (Crowson, 1984; Newton, 1984; Wheeler and Blackwell, 1984).

Stand age also influences faunal structure in new CWM. The number of species, genera, and families collected from wood in old-growth stands was higher than corresponding samples from mature stands (Table 5-2). This pattern may indicate that the fauna in old stands is more diverse than in mature stands. However, previous and concurrent studies in the same forest stands have shown that arthropod diversity in old and mature stands are often similar, but that there is high turnover in species composition (see Chapters 3 and 4; Spence et al., 1996, 1997). Tree stem density is much higher in mature forest stands than old stands and CWM volume is higher in old stands (Stelfox, 1995), which may make it easier for beetles to find suitable CWM 'islands' in old stands. Overall, abundance did not vary with stand age, but predators comprised a higher proportion of the fauna in old stands than in mature stands (Table 5-4). This is similar to the trends seen in Chapters 3 and 4, and may reflect a turnover in saproxylic community structure across stand ages.

The type of wood section, snags, logs or stumps, did not affect beetle taxon richness or abundance (Table 5-2), but did have a large effect on faunal trophic composition. Wood boring beetles represented a significantly higher proportion of the fauna in snags than in logs and stumps (Tables 5-4 and 5-5). This reflects host selection behaviour of wood- and bark-boring beetles, many of which are attracted to dark, vertical silhouettes (Amman and Cole, 1983; Raffa and Berryman, 1980). Of the five taxa collected exclusively from snags, three were wood borers (Table 5-1), suggesting that wood borers colonize wood mainly by flight. Predators formed a significantly higher proportion of the fauna in logs and stumps, than in snags (Table 5-4). Many of these species, especially carabids and staphylinid beetles, readily disperse by walking rather than flying (see Chapter 3). These trends are similar to a related study of the beetle CWM fauna of dead pines and spruces in Finland, which showed that a large number of beetles were selective for logs rather than snags (Väisänen et al., 1993).

5.5.2 Influence of arthropods on decay processes

Wood hardness readings indicated that screened and unscreened wood sections were similar in amount of decay, suggesting that in boreal ecosystems *Populus* decay is a long process. The half time for aspen log mineralization has been measured between 10 years (Gosz, 1980) and 14 years (Miller, 1983); and it takes anywhere between 43-60 years for poplar logs in forests to lose 95% of its mass, whereas in aquatic systems it may take greater than 250 years (Gosz, 1980; Miller, 1983). It has also been suggested that insects only begin to invade new wood when between 60-90% of dry weight has been lost (Swift, 1977). This doesn't seem to be the case in *Populus* because two-year-old wood sections seemed as heavy as when they were cut, although the weights were not measured. Wood sections sampled from old stands seemed to be slightly softer than mature stands, although not significantly. This may be due to large diameter trees containing significantly more heart rot than is found in smaller diameter trees found in mature stands. Evidence suggests that significant decay does not occur between year 1 and year 2, and that insects do not speed the decay process initially. It may be over the long term that one sees the influence of arthropods on wood decay.

Many studies have looked at the effects of insects and fungi on the long term rate of decay in wood and how they regulate nutrient flow back to the forest floor (Fager, 1968; Ausmus, 1977; Reichle,1977; Swift, 1977; Deyrop, 1981; Harmon et al, 1986; Vogt et al, 1986; Alban and Pastor, 1993; Kauffman et al, 1993). In general, wood decomposition has three stages: fungi attacks the wood through the pith, invertebrates channel into the wood introducing other fungi and bacteria, and then secondary colonizers attack the wood (Ausmus, 1977). In Alberta, *Populus* decomposition may follow a sequence such as: 1) fungi, including heart rots and stains, enter weakened trees and recently killed trees through the root system, resulting in an initial loss of nutrients from the wood. Sloughing of some bark may or may not occur, at least in *Populus*; and 2) various wood borers such as *T. retusum*, *P. mucronatus*, *A. liragus* and *Trachysida mutabilis* (Newman) colonize the wood, acting as primary channelers and vectors of fungi. Indirect introduction of fungi and bacteria also occurs during wood boring and insect feeding, resulting in competition between different ascomycete and basidiomycete fungi and nitrogen fixing and cellulytic bacteria. Other invertebrate species begin feeding under the bark, gaining entry through wood borer holes and cracks in the bark. There is also evidence to suggest that some beetle species, such as *T. retusum, P. piceus, E. biguttata,* and *M. cylindrica* are found primarily in the most recently killed trees. Because this study focused on the beginning of the decomposition process, secondary colonizers of dead wood were not seen (see Chapters 3 and 4).

Wood decomposition represents a long-term stabilizing force within boreal mixedwood forests. Mattson and Addy (1975) suggest that insects serve as regulators of energy flow and biochemical synthesis in the ecosystem. Clearly, invertebrates, and their associated wood fungi have very important roles in this ecosystem by facilitating breakdown of dead organic matter and return of nutrients to the soil. In other forested ecosystems the availability of wood substrates, and the alternating pattern of nutrient source and sink, both seasonally and over decades, greatly influence forest nutrient cycling mechanisms (Ausmus, 1977; Swift, 1977). For example, soil organic matter in and beneath logs greatly influence root distribution and uptake, and spruce development is often dependent on the availability of woody material with perched water tables (Ausmus, 1977). This study provides a good introduction to invertebrates involved in *Populus* wood breakdown, but much more information is required about the complex interaction between taxa and the roles these organisms play in nutrient cycling in boreal mixedwood forests.

Table 5-1. The standardized abundance of Coleoptera collected from new coarse woody material from two ages of boreal
mixedwood forest near Lac la Biche and Eureka River, Alberta in 1994 and 1995.
Abundance has been standardized to 150 rearing days and 0.1 m3 of wood.
(* 1-5 individuals; ** 6-20 individuals; *** 21-100 individuals; **** >100 individuals)

		LOG		STUMP		SNAG	
Family	**Species**	**1994**	**1995**	**1994**	**1995**	**1994**	**1995**
Bostrichidae	*Endecatomus rugosus* (Randall)						*
Buprestidae	*Agrilus liragus* Bart.&Brwn.	**				**	
Carabidae	*Agonum obsoletum* Say				*		
	Platynus decentis (Say)				*		*
	Psydrus piceus LeConte		*				
	Trichocellus cognatus (Gyllenhal)					*	
Cerambycidae	*Trachysida mutabilis* (Newman)						*
Cerylonidae	*Cerylon castaneum* Say		**		*		
Corylophidae	*Molamba biguttata* (LeConte)	****	*	***	**	****	**
	Orthoperus scutellaris LeConte		*			*	
Cryptophagidae	*Atomaria (Anchicera) ephippiata* Zimmerman		*		***		
	Atomaria (Anchicera) spp.	**	*	**	*		**
	Antherophagus ochraceus Melsheimer				*		
	Atomaria (Atomaria) spp.		*		*		
	Cryptophagus acutangulus Gyllenhal	**		*		*	
	Cryptophagus tuberculosis Maklin				*		*
	Henoticus spp.		**	*	*	*	
Cucujidae	*Cucujus clavipes* Fab.		*	**	**		**
	Laemophloeus biguttatus (Say)	*					
Dermestidae	*Dermestes lardarius* L.		*	*			
	Megatoma cylindrica Kirby		*				
	Trogoderma sinistrum Fall	*					
Endomychidae	*Endomychus biguttata* Say		**				
Histeridae	*Platysoma lecontei* Marseul			*			
Lampyridae	*Pyractomena borealis* (Randall)			*			
Lathridiidae	*Corticaria* sp A		***		**		**
	Corticaria sp D			**		*	
	Corticaria sp E	**	**	**	**	**	***
	Enicmus sp A			*			
	Lathridius sp A					*	
	Melanopthalma pumilla (LeConte)		*	*			
Leiodidae	*Agathidium* spp		**				
Lymexylidae	*Hylecoetus lugubris* Say				*		
Melandryidae	*Enchodes sericea* (Haldeman)			*			
Micropeplidae	*Micropeplus laticollis* Maklin		*				
Nitidulidae	*Epuraea* spp.		*	**	*	*	
	Glischrochilus moratus Brown			*		**	
Pselaphidae	*Batrisodes* spp.			*	*		
	Euplectus duryi Casey		**	*	***		
Ptiliidae	*Acrotrichus* spp.			*	**	*	
Pyrochroidae	*Dendroides testaceus* LeConte				*		
Rhizophagidae	*Rhizophagus bruneus* Horn	***	***	*	*	*	
	Rhizophagus remotus LeConte	****	***	****	***	****	*
Scolytidae	*Procryphalus mucronatus* (LeConte)						**
	Trypodendron retusum (LeConte)	****		****		****	
Staphylinidae	Aleocharinae	**	***	**	***	**	**
	Atrechus macrocephalus (Nordm.)				*		
	Carphacis nepigonensis (Bernhauer)			*			
	Nudobius cephalus (Say)	*	**		**		
	Phloeonomus lapponicus (Zetterstedt)		*	**		*	
	Pseudopsis sagitta Herman	*	**				
	Quedius plagiatus Mannerheim		**	*			*
	Quedius velox Smetana		*		*		
	Sepedophilus littoreus (L.)				*	*	
	Sepedophilus testaceus (Fab.)		**				
Trogossitidae	*Thymalus marginicollis* Chevrolat						*

Table 5-2. Mean (±standard error) number of families, genera, species, and standardized abundance of beetles colonizing newly created sections of coarse woody material sections in old and mature aspen-mixedwood forest stands near Lac la Biche and Eureka River, Alberta. See Appendix 10 for analysis of variance.

	Eureka River	Lac la Biche	Old stands	Mature stands	Screened	Unscreened	Log section	Snag section	Stump section	1994	1995
Number of Families	2.22±0.28	2.15±0.23	2.78±0.25	1.59±0.25	1.38±0.17	2.99±0.17	2.22±0.21	1.97±0.21	2.36±0.21	2.46±0.15	1.91±0.15
Number of Genera	2.35±0.38	2.38±0.31	3.09±0.34	1.65±0.34	1.43±0.21	3.31±0.21	2.45±0.26	2.05±0.26	2.60±0.26	2.54±0.20	2.20±0.20
Number of Species	2.54±0.40	2.50±0.33	3.35±0.37	1.68±0.37	1.56±0.22	3.47±0.22	2.71±0.27	2.15±0.27	2.69±0.27	2.74±0.24	2.29±0.24
Abundance	25.75±7.85	31.10±6.41	22.31±7.17	34.55±7.17	7.37±7.17	49.48±7.17	19.82±8.79	43.52±8.79	21.94±8.79	45.22±6.12	11.64±6.12

Table 5-3. Mean (±standard error) number of families, genera, species, and standardized abundance of significant main effect interactions of beetles colonizing newly created sections of coarse woody material sections in old and mature aspen-mixedwood forest stands near Lac la Biche and Eureka River, Alberta. See Appendix 10 for analysis of variance.

Source	**Level**	**Species Mean±SE**	**Genera Mean±SE**	**Families Mean±SE**	**Abundance Mean±SE**
Year*Age	1994-Mature	-	2.18±0.29	2.09±0.21	61.12±8.66
	1995-Mature	-	1.12±0.29	1.09±0.21	7.99±8.66
	1994-Old	-	2.30±0.29	2.83±0.21	29.32±8.66
	1995-Old	-	3.27±0.29	2.73±0.21	15.29±8.66
Y*T	1994-Screen.	-	-	-	10.42±8.79
	1994-Unscreened	-	-	-	80.02±8.79
	1995-Screen.	-	-	-	4.33±8.79
	1995-Unscreened	-	-	-	18.94±8.79
Year*Section	1994-Log	2.60±0.33	2.21±0.33	2.20±0.29	22.57±10.77
	1994-Snag	2.95±0.33	2.81±0.33	2.73±0.29	81.24±10.77
	1994-Stump	2.66±0.33	2.60±0.33	2.45±0.29	31.84±10.77
	1995-Log	2.81±0.33	2.71±0.33	2.25±0.29	17.08±10.77
	1995-Snag	1.35±0.33	1.29±0.33	1.22±0.29	5.79±10.77
	1995-Stump	2.72±0.33	2.60±0.33	2.27±0.29	12.04±10.77

Table 5-4. Mean (±standard error) proportion of fungivores, predators, wood borers, scavengers and unknown roles of beetles colonizing newly created sections of coarse woody material sections in old and mature aspen-mixedwood forest stands near Lac la Biche and Eureka River, Alberta. See Appendix 11 for analysis of variance.

Trophic Role	Eureka River	Lac la Biche	Old stands	Mature stands	Screened	Unscreened	Log section	Snag section	Stump section	1994	1995
Fungivores	36.29±5.31	27.38±4.34	35.58±4.85	28.10±4.85	29.16±4.45	34.51±4.45	22.19±5.45	39.10±5.45	34.22±5.45	29.57±8.35	34.11±8.35
Predators	36.15±4.27	27.66±3.48	38.57±3.89	25.24±3.89	31.45±4.23	32.36±4.23	46.79±5.18	14.51±5.18	34.41±5.18	37.73±5.65	26.08±5.65
Wood Borers	8.66±3.86	14.98±3.15	9.98±3.52	13.66±3.52	6.10±2.59	17.54±2.59	7.16±3.17	20.32±3.17	7.98±3.17	19.57±2.62	4.07±2.62
Scavengers	2.13±1.25	0.57±1.02	2.51±1.14	0.19±1.14	0.34±1.18	2.36±1.18	3.76±1.45	0.02±1.45	0.27±1.45	0.22±1.16	2.48±1.16
Unknown	8.42±2.75	5.77±2.21	6.62±2.47	7.57±2.47	5.84±2.52	8.35±2.52	9.66±3.08	4.15±3.08	7.47±3.08	3.16±3.16	11.03±3.16

Table 5-5. Summary of main effect interactions of the mean (±standard error) proportion of fungivores, predators, wood borers, scavengers and unknown roles of beetles colonizing newly interactions of beetles colonizing newly created sections of coarse woody material sections in old and mature aspen-mixedwood forest stands near Lac la Biche and Eureka River, Alberta. See Appendix 11 for analysis of variance.

Trophic Role	Source	Level	Mean (%) ±SE
Predators	Section*Age	Log-Mature	27.98±7.33
		Snag-Mature	13.92±7.33
		Stump-Mature	33.82±7.33
		Log-Old	65.60±7.33
		Snag-Old	15.12±7.33
		Stump-Old	35.01±7.33
Wood Borers	Year*Region	1994-Eureka River	10.85±4.06
		1994-Lac la Biche	28.29±3.31
		1995-Eureka River	6.48±4.06
		1995-Lac la Biche	1.66±3.31

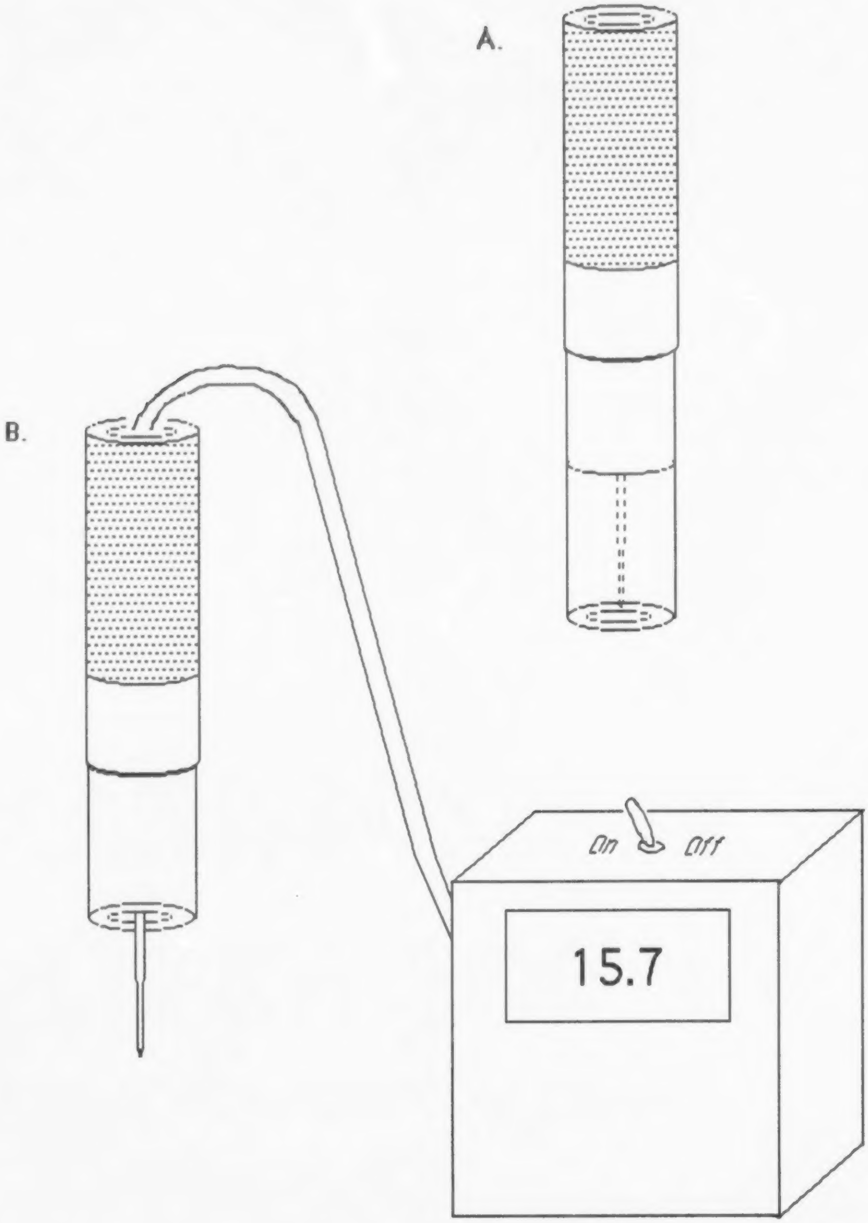

Figure 5-1. The h-gun, used for taking quantitative wood hardness measurements from snag, log, and stump wood sections. Wood hardness measurements are inversely proportional to amount of decay.
A. h-gun in resting position;
B. h-gun in fired position.

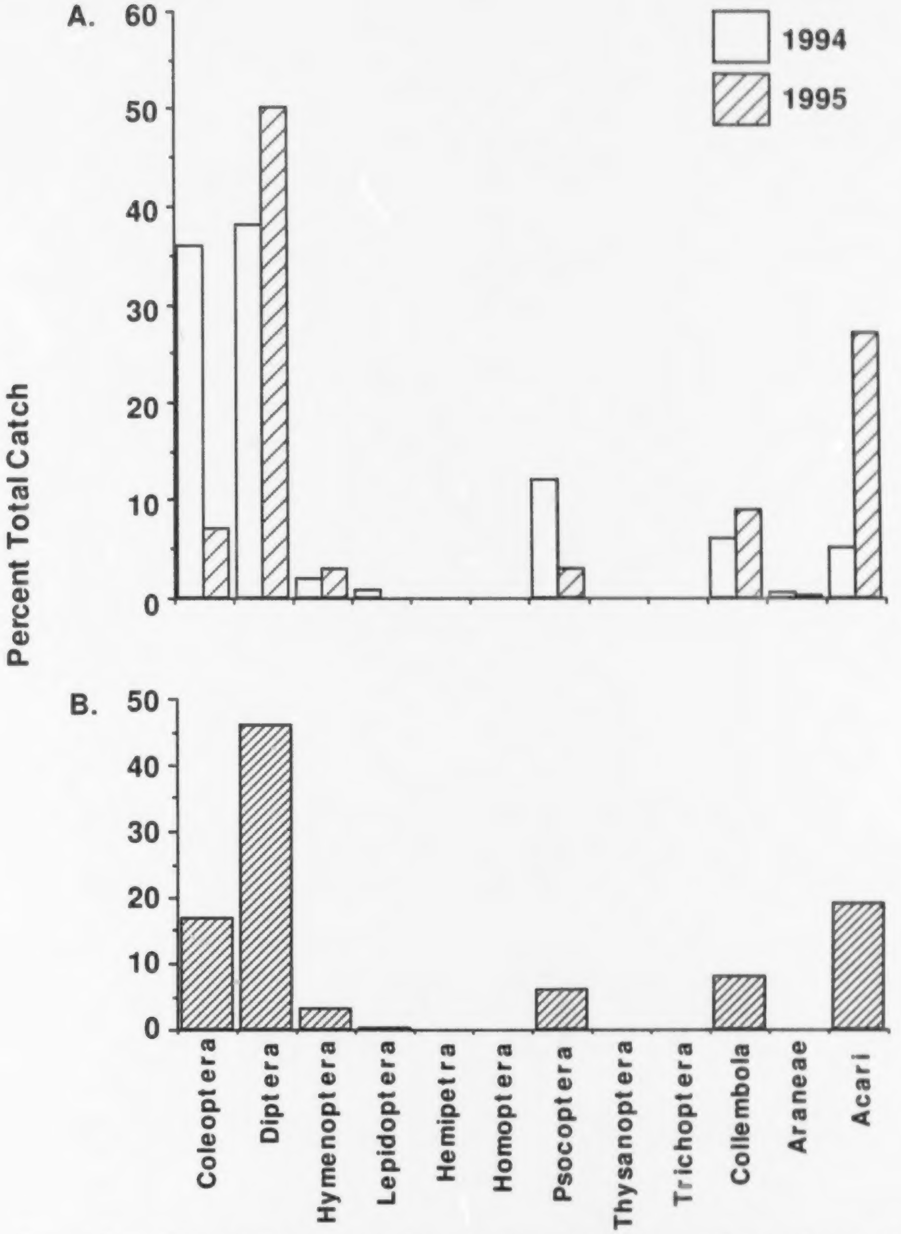

Figure 5-2. The relative proportion of arthropod orders collected by rearings from new coarse woody material:

A. data from wood sections reared in 1994, after one year of exposure; and wood sections reared in 1995, two years after exposure.

B. data from both years combined.

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6. Summary and Recommendations

6.1 Summary

This thesis has stemmed from concerns that large scale forest development has detrimental effects upon ecosystem productivity and structure, resulting from a loss of habitat and consequent loss of biodiversity. By focusing on one forest community, the arthropods that act to breakdown coarse woody material (CWM) and mobilize nutrients for export to the soil, I have been able to show that large scale habitat disturbance, associated with forestry development, may in fact be detrimental to this community.

The first step in understanding ecosystem function is cataloging the diversity of organisms found. There is a large and dynamic arthropod community associated with *Populus* dead wood (Chapter 2). Over 39,000 arthropod specimens were collected over the three years of this study. The Coleoptera, which make up between 25-35% of this fauna, were the main focus of analysis of community structure, temporal and spatial variation, and the impacts of forest harvesting. It soon became evident that little information, both taxonomic and ecological, existed for many of the beetle species collected. A large number of the 372 beetle taxa collected were new provincial records, newly described, or were unidentifiable.

Arthropods associated with CWM can be classified into two broad categories: saproxylic species, which are directly dependent on wood, wood fungi and other plants, and other saproxylics for food; and species which use dead wood as shelter, overwintering sites and foraging and would probably not be seriously harmed by the loss of dead wood. Fungivores and predators were the trophic roles which dominated beetle assemblages from CWM.

Two collecting methods were used to census the arthropods from dead wood, rearing of specimens from CWM and flight intercept traps attached to snags. Both methods worked well, but each method had its own bias, and these have to be considered when choosing a sampling method. Rearings allowed me to sample only those insects in the wood at time of collection, whereas, window-traps measure flight activity of insects to and from snags. There are also practical factors to consider such as cost, labour involved in building rearing cages and window-traps, sampling effort and data return, replicability, and reliability. To census an entire community, a combination of trapping methods is recommended.

The beetle community differed considerably across spatial scales (Chapter 3). Few differences were noted in relative species richness and abundance within a particular spatial scale, instead it seemed a large number of beetle species were restricted to specific regions, forest stand age classes, decay classes and sample types (logs or snags). A large number of beetle species also showed preferences for wood in a particular stand age or decay class, as shown by the old-growth dependency index and the large number of species collected only from a particular decay class. Analysis of beetle trophic roles showed that community structure is rather conservative, despite the fact that there is high species turnover across regions. There also was a succession in beetles filling certain trophic roles across stand age, with mature stands being dominated by fungivores, and old-growth stands dominated by predators. Detrended correspondence analysis suggested that biotic and abiotic factors associated with decay class, followed by region, and stand age were the prime determinants in the distribution of wood-inhabiting beetles across the landscape.

Temporal variation is also an important consideration when sampling a community. Faunal similarity for rearings between 1993 and 1994 was only 21%, whereas, the fauna from window-traps was 73% between 1994 and 1995. A total of 42, 51 and 17 species were unique to each of 1993, 1994 and 1995 respectively. Parametric data analysis of the number of taxa (i.e. species, genera, families) and standardized abundance also showed significant differences across years (see Chapter 3). The fact that new species continued to be trapped in the third year of sampling suggests that there are likely more species which belong to this community that have yet to be sampled. This highlights the need to monitor insect communities over several years to inventory species or to assess the impacts of ecosystem disturbance.

A study of the effects of harvesting on the saproxylic fauna was initiated in 2-year-old cutblocks near Lac la Biche (Chapter 4). Species richness and abundance increased in harvested stands, but a number of species that were found in forested stands were absent from harvested areas. Age of stand before harvesting affected very little community structure after harvesting, except that old forest stands and old stands that were harvested seemed more similar with respect to the beetle fauna than their associated mature stands, suggesting that saproxylic faunas survive at least two years post-harvest. There also seemed to be little faunal difference between decay classes, except for wood in decay class 1 which had a significantly higher abundance of beetles, presumably due to all the fresh woody material after harvest. Harvesting had little initial effect on trophic role composition. Detrended correspondence analysis suggested biotic and abiotic factors associated with harvested and forested stands primarily influenced the distribution of beetles, followed by factors associated with stand age.

The role that arthropods play in initiating and regulating wood decomposition was studied experimentally in Chapter 5. Healthy trees were cut and either exposed to insect attack, or were covered with insect screen to prevent insect colonization. A large number of arthropods and beetles were collected from this wood, mainly from the Coleoptera, Diptera, Psocoptera and Acari. Wood borer colonization may predispose the wood for colonization by arthropods because the proportion of soil arthropods greatly increased in the second year of exposure. Focusing on the Coleoptera, I found four beetle species that seemed restricted to recently dead wood. Wood section (i.e. snag, stump, and log) had quite an effect on the beetles colonizing the wood, with predators preferring logs and stumps, fungivores preferring snags and stumps, and wood boring beetles equally expressed in each wood section. Time of exposure of the wood (one or two years) also affected the fauna present, with wood borers showing a clear preference for one year old dead wood, and scavengers showing a preference for two year old dead wood. *Trypodendron retusum* (LeConte), an ambrosia beetle was identified as the primary channeler species regulating initial decomposition. The treatment and control wood did not significantly differ with respect to amount of decay, suggesting that insects, at least in the first two years of wood death, do not significantly increase the rate of decomposition. It was hypothesized that over the long term, 40-80 years, that colonization by arthropods would have a significant effect on decomposition. The amount of decay also did not significantly differ across the two years, confirming that wood decomposition in boreal ecosystems is a long process.

6.2 General discussion and recommendations

As the human race continues to increase in numbers, a higher demand will be placed on the Earth's natural resources. Biological diversity was considered at an all-time high just prior to the industrial revolution, where biological resources were freely available for exploitation to support industrial development (McNeely, 1989). It has only been recently, in the last half of the 20th century, when it has been realized that biological resources have limits and that we are exceeding those limits. Expected population increases to 8 billion people are estimated for the year 2025 (Wilson, 1992). Demands for raw materials, such as wood, metals, fuels, land, and food are increasing, requiring exploitation of previously uninhabited areas resulting in subsequent losses in species diversity. It has been recognized for some time that the taxa that comprise ecosystems are the building blocks responsible for the health and resilience of an ecosystem to disturbance. Subsequent losses in species numbers is then directly related to the deterioration of critical functions within ecosystems (Naeem et al., 1994). Solving these problems requires research that increases communication between conservationists and land managers to discuss the issues, choices, and consequences involved in particular management decisions. Information required before making these decisions requires a thorough understanding of the biological diversity of a given area, the temporal and spatial scales that these taxa are sensitive to, and the effects of habitat disturbance on the fauna present (Noss, 1983; McNeely, 1989; Boyle, 1991; Hammond, 1992).

As forest harvesting continues in the boreal forests of Canada, there will be continued concern over the sustainability of this resource. Forest management currently focuses on the 'natural disturbance' model which suggests that harvesting should emulate the pattern of forest fires across the landscape (Hansen et al., 1991; Probst and Crow, 1991; Hunter, 1993). It has been argued that the biota found in these forest types are adapted to periodic natural disturbances that create shifting mosaics of forest across the landscape. Fires also create stands that are different in physical structure than harvested stands, and these differences in biotic and abiotic factors may greatly influence the arthropod fauna present (Barnes et al., 1989; Haila et al., 1994). Woody material of all decay stages are often abundant after a forest fire clears an area because not all wood on the site is consumed, leaving what has been termed an "ecological foot print" of the previous stand (Stelfox, 1995). Whereas in forestry operations all merchantable tree biomass is removed from cutblocks, and unmerchantable wood is removed, piled and/or burned because it is considered as a safety hazard or interferes with re-planting (Stelfox, 1995).

Conservation of arthropod assemblages from CWM, a fauna that has been shown to be sensitive to forest harvest (Heliövaara and Väisänen, 1984; Speight, 1989; Väisänen et al., 1993; Siitonen and Martikainen, 1994), should consider several factors. First, the beetle community associated with *Populus* CWM is not homogeneous geographically. It was shown in Chapters 2 and 3 that the beetle community developed differently across wide geographical regions. The fauna collected from Eureka River had many more species associated with northern and montane sites, whereas, the Lac la Biche fauna had more species in common with lowland forest sites. These data support findings from other arthropod community studies in these forests (Langor et al., 1993; Spence and Langor, 1994; Spence et al., 1996, 1997). These data suggest that reserve areas, accounting for as much variation in forest structure, should be set up across the landscape.

Truncation of forest stand age structure may have serious consequences for the fauna dependent on CWM in old-growth stands. A paradigm that has developed over the years is that management should focus on increasing species diversity in managed forests. In contrast recent research from Finland suggests that the focus of conservation efforts should be on species limited to certain habitat types rather than managing for increased diversity (Väisänen et al., 1993). The data presented in this thesis has shown that there are saproxylic beetles that seem restricted to both old and mature stand ages. Therefore maintaining a mosaic of stand age structures across the landscape, similar to a landscape created by natural fire dynamics, may act to preserve specialist species. In addition, connectivity between forest fragments should be increased to allow species with poor dispersal abilities to move freely between forest fragments (Chapters 3 and 5; Ås, 1993; Berg et al., 1994).

The decay stage of the wood and whether the wood was standing or fallen had an influence on beetle species present. In Chapter 3 I was able to show that factors such as the fungal community, temperature, and moisture regimes associated with different decay classes influenced the distribution of beetles across the landscape. Newly created dead wood, as well as snags, logs and stumps, harboured a unique beetle fauna (Chapters 3 and 5). The ephemeral nature of some decay classes, and the finding that snag and log densities change considerably across the landscape (Stelfox, 1995), suggest that existing snags and logs should be left in cut blocks in an attempt to maintain stand structure. This wood could act as refugia for species presently in the stand, and act as sources of new colonization in the developing stand. Leaving individual and clumps of live trees in cutblocks, that will become CWM later in stand succession, may also help preserve specialist species.

Finally, adequate assessment of the fauna from CWM requires several years of effort. In Chapters 2 and 3 I was able to show that the beetle fauna collected changed considerably across years. Insect populations often show some form of periodicity (Taylor, 1986). Also, abiotic factors such as weather and natural disturbances can alter population sizes in any given year (Bonan and Shugart, 1989). Therefore, temporal variation must be considered when sampling insect communities.

6.3 Recommendations for future research

This thesis is a starting point for further study of arthropods associated with coarse woody material and their associated decay fungi and bacteria. The focus of this research has been on the Coleoptera, but many arthropod groups have been collected from wood. Diptera, Hymenoptera, Psocoptera and soil organisms such as Collembola and the Acari were collected in significant numbers and warrant further research. Although an attempt was made at identifying the interactions between beetles and fungi, much more work is required to understand their interactions in the breakdown of woody material. Further research should also focus on the succession of arthropods from stands of pyrogenic origin to follow how the community develops through burned stands to 'old' stands. Finally, the effects of man-made disturbance such as forest harvesting and oil and gas exploration should be studied and compared to natural processes to evaluate and preserve this important fauna.

6.4 Literature cited

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Appendix 1. Analysis of variance comparing the number of species, genera, families, and standardized abundance from saproxylic beetles reared from *Populus* coarse woody material, from Lac la Biche and Eureka River (Region); old and mature stands (Age); three decay classes of wood (Decay Class); snags and logs (Type); and 1993 and 1994 (Year).

(^{a}all three factor and higher interactions of region, age, decay class, and type pooled to form error;

^{b}all three factor and higher interactions pooled to form error; † denotes significance at 95%).

		Species			Genera			Families			Abundance		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	36.75	0.88	0.3715	22.68	0.53	0.4864	2.08	0.19	0.6768	1892.40	0.15	0.7086
Age (A)	1	432.00	10.40	0.0104 †	438.02	10.17	0.0110 †	140.08	12.47	0.0064 †	206707.60	16.26	0.0030 †
R*A	1	27.00	0.65	0.4409	20.02	0.46	0.5126	7.52	0.60	0.4581	200699.70	15.79	0.0032 †
Decay Class (DC	2	65.27	1.57	0.2598	53.52	1.24	0.3338	46.08	2.43	0.1436	31696.81	2.49	0.1375
R*DC	2	73.93	1.78	0.2232	69.93	1.62	0.2500	30.58	1.45	0.2836	40595.30	3.19	0.0895
A*DC	2	20.43	0.49	0.6269	14.02	0.33	0.7303	20.33	1.83	0.2149	66094.50	5.20	0.0316 †
Type (T)	1	24.08	0.58	0.4659	22.68	0.53	0.4864	25.52	2.14	0.1771	15977.60	1.26	0.2913
R*T	1	0.08	0.01	0.9653	0.52	0.01	0.9149	13.02	0.01	0.9332	32781.68	2.58	0.1428
A*T	1	21.33	0.51	0.4918	17.52	0.41	0.5395	3.52	0.19	0.6768	585.21	0.05	0.8349
DC*T	1	3.77	0.09	0.9140	4.93	0.11	0.8930	3.58	0.83	0.4665	57394.46	4.51	0.0439 †
Error^a	9	41.53			43.07			78.68			12713.00		
Year (Y)	1	954.08	48.83	0.0001 †	981.02	56.92	0.0001 †	120.33	9.63	0.0061 †	1091848.80	42.03	0.0001 †
Y*R	1	18.75	0.96	0.3403	17.52	1.02	0.3267	27.00	2.16	0.1588	2664.10	0.10	0.7525
Y*A	1	33.33	1.71	0.2080	54.18	3.14	0.0931	0.33	0.03	0.8721	139889.20	5.38	0.0323 †
Y*DC	2	14.02	0.72	0.5014	10.02	0.58	0.5692	7.58	0.61	0.5557	39955.40	1.54	0.2418
Y*T	1	14.08	0.72	0.4070	25.52	1.48	0.2394	16.33	1.31	0.2678	15931.60	0.61	0.4438
Error^b	18	19.53			17.23			12.49			25979.90		

Appendix 2. Analysis of variance comparing the number of species, genera, families, and standardized abundance from saproxylic beetles collected with window-traps from *Populus* snags, from Lac la Biche and Eureka River (Region); old and mature stands (Age); three decay classes of wood (Decay Class); snags and logs (Type); and 1994 and 1995 (Year). ([a]stands within region by age interaction; [b]decay class by stands within region by age interaction; [c]year by stand within region by age; [d]decay class by year by stand within region by age interaction; † denotes significance at 95%).

		Species			Genera			Families			Abundance		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	52.56	0.08	0.7877	60.06	0.12	0.7432	55.00	0.25	0.6403	924495.07	1.34	0.3119
Age (A)	1	403.34	0.64	0.4698	253.34	0.52	0.5107	122.84	0.57	0.4927	277372.16	0.40	0.5609
R*A	1	11.67	0.02	0.8986	0.34	0.00	0.9802	7.56	0.04	0.8607	25489.29	0.04	0.8571
Error[a]	4	634.17			487.03			215.97			691371.30		
Decay Class (DC	2	0.90	0.02	0.9786	0.77	0.02	0.9756	1.02	0.11	0.8933	361001.80	2.58	0.1362
R*DC	2	102.52	2.48	0.1452	96.75	3.09	0.1015	43.96	4.93	0.0402 †	109202.80	0.78	0.4896
A*DC	2	196.92	4.76	0.0434 †	168.69	5.38	0.0330 †	69.67	7.81	0.0131 †	41233.97	0.30	0.7521
R*A*DC	2	5.13	0.12	0.8849	10.77	0.34	0.7190	0.89	0.10	0.9055	152771.10	1.09	0.3802
Error[b]	8	41.34			31.34			8.91			139666.80		
Year (Y)	1	502.50	3.09	0.1536	423.67	3.57	0.1319	130.34	2.63	0.1802	106820.68	1.04	0.3648
R*Y	1	16.67	0.10	0.7649	8.50	0.07	0.8022	0.06	0.00	0.9734	52639.65	0.51	0.5130
A*Y	1	134.17	0.82	0.4151	146.00	1.23	0.3297	62.67	1.26	0.3237	275088.36	2.69	0.1766
R*A*Y	1	1.56	0.01	0.9266	5.84	0.05	0.8354	14.06	0.28	0.6225	1560.54	0.02	0.9077
Error[c]	4	162.64			118.75			49.56			102400.50		
DC*Y	2	2.29	0.11	0.8994	4.69	0.27	0.7698	1.21	0.13	0.8782	17265.59	0.14	0.8705
R*DC*Y	2	54.67	2.56	0.1386	53.86	3.10	0.1006	6.43	0.70	0.5250	133638.47	1.09	0.3807
A*DC*Y	2	3.54	0.17	0.8500	5.52	0.32	0.7361	2.75	0.30	0.7492	21728.81	0.18	0.8405
R*A*DC*Y	2	14.39	0.67	0.5369	19.52	1.12	0.3711	2.64	0.29	0.7577	46450.49	0.38	0.6958
Error[d]	8	21.39			20.45			12.05			137084.10		

Appendix 3. Analysis of variance comparing mean standardized abundance of saproxylic beetles in each trophic role reared from *Populus* coarse woody material, from Lac la Biche and Eureka River (Region); old and mature stands (Age); three decay classes of wood (Decay Class); snags and logs (Type); and 1993 and 1994 (Year).

(^{a}all three factor and higher interactions of region, age, decay class, and type pooled to form error; ^{b}all three factor interactions pooled to form error; † denotes significance at 95%).

		FUNGIVORE			PREDATOR			WOOD BORERS			SCAVENGERS			UNKNOWN		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	161.16	0.04	0.8417	449.82	0.30	0.5996	2303.89	0.36	0.5610	7.05	0.07	0.7985	15067.21	4.50	0.0630
Age (A)	1	43273.15	11.35	0.0083 †	37.30	0.02	0.8789	318.61	0.05	0.8274	882.69	8.65	0.0165 †	42097.59	12.57	0.0063 †
R*A	1	31031.02	8.14	0.0190 †	13720.09	9.03	0.0148 †	6351.35	1.00	0.3424	919.72	9.01	0.0149 †	41646.39	12.43	0.0065 †
Decay Class (DC)	2	7956.23	2.09	0.1800	2887.43	1.90	0.0205	16646.87	2.63	0.1258	130.81	1.28	0.3239	4147.65	1.24	0.3350
R*DC	2	3596.58	0.94	0.4246	3844.75	2.53	0.1343	1027.51	0.16	0.8525	144.92	1.42	0.2912	5381.86	1.61	0.2532
A*DC	2	13150.40	3.45	0.0772	3887.62	2.56	0.1319	1912.69	0.30	0.7462	596.48	5.84	0.0236 †	2314.82	0.69	0.5258
Type (T)	1	157.37	0.04	0.8435	2562.49	1.69	0.2263	14383.27	2.27	0.1658	41.38	0.41	0.5402	2599.12	0.78	0.4013
R*T	1	3279.51	0.86	0.3779	25.38	0.02	0.9000	3022.81	0.48	0.5068	0.86	0.01	0.9288	3949.15	1.18	0.3058
A*T	1	31.88	0.01	0.9291	202.97	0.13	0.7232	229.06	0.04	0.8533	46.22	0.45	0.5179	52.62	0.02	0.9030
DC*T	1	2548.61	0.67	0.5361	1687.45	1.11	0.3706	10389.83	1.64	0.2464	227.04	2.22	0.1641	3908.96	1.17	0.3543
Error^a	9	3811.97			1519.32			6323.41			169.87			3350.00		
Year (Y)	1	145488.02	27.00	0.0001 †	13915.37	7.83	0.0119 †	27330.53	4.20	0.0554 †	3898.18	22.95	0.0001 †	100976.72	22.79	0.0002 †
Y*R	1	5996.33	1.11	0.3054	1496.86	0.84	0.3710	1727.90	0.27	0.6127	15.75	0.09	0.7642	10426.29	2.35	0.1424
Y*A	1	16719.31	3.10	0.0951	10.07	0.01	0.9408	681.16	0.10	0.7501	950.63	5.60	0.0294 †	34080.51	7.69	0.0125 †
Y*DC	2	9732.45	1.81	0.1928	1923.72	1.08	0.3600	13643.01	2.10	0.1521	101.51	0.60	0.5607	2608.21	0.59	0.5654
Y*T	1	1540.12	0.29	0.5994	939.09	0.53	0.4767	5042.17	0.77	0.3905	8.50	0.05	0.8255	2453.08	0.55	0.4664
Error^b	18	5387.53			1777.86			6512.18						4430.33		

Appendix 4. Analysis of variance comparing mean standardized abundance of saproxylic beetles in each trophic role collected with window-traps from *Populus* snags, from Lac la Biche and Eureka River (Region); old and mature stands (Age); three decay classes of wood (Decay Class); snags and logs (Type); and 1994 and 1995 (Year).

([a]stands within region by age interaction; [b]decay class by stands within region by age interaction; [c]year by stand within region by age; [d]decay class by year by stand within region by age interaction; † denotes significane at 95%).

Source	df	FUNGIVORES			PREDATORS			WOOD BORERS			SCAVENGERS			UNKNOWN		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	554350.36	8.90	0.0406 †	35912.59	0.21	0.6724	1.01	0.00	0.9911	73.61	0.29	0.6202	2180.04	0.96	0.3821
Age (A)	1	60770.59	0.98	0.3791	289346.09	1.67	0.2657	18385.7	2.54	0.1862	312.31	1.22	0.3313	0.08	0.00	0.9955
R*A	1	204535.87	3.29	0.1441	73764.21	0.43	0.5495	1324.48	0.18	0.6908	415.66	1.62	0.2716	15.42	0.01	0.9382
Error[a]	4	62259.25			173104.72			7237.01			256			2264.66		
Decay Class (DC	2	7714.59	0.45	0.6520	238993.61	3.50	0.0810	5425.31	2.40	0.1526	365.75	5.19	0.0358 †	929.43	4.49	0.0493 †
R*DC	2	21448.47	1.25	0.3357	12638.08	0.18	0.8346	2523.01	1.12	0.3738	94.96	1.35	0.3128	1643.05	7.94	0.0126 †
A*DC	2	19730.11	1.15	0.3627	17084.56	0.25	0.7846	2380.68	1.05	0.3927	236.33	3.36	0.0874	113.02	0.55	0.5994
R*A*DC	2	15761.34	0.92	0.4361	94759.93	1.39	0.3040	3275.38	1.45	0.2905	12.45	0.18	0.8411	806.20	3.90	0.0659
Error[b]	8	17092.06			68331.09			2261.15			70.41			206.97		
Year (Y)	1	13656.66	0.48	0.5258	2265.36	0.09	0.7839	42859.4	15.40	0.0172 †	357.37	1.09	0.3550	3132.87	1.37	0.3066
R*Y	1	446.88	0.02	0.9061	41733.92	1.58	0.2766	469.17	0.17	0.7024	147.25	0.45	0.5391	2696.30	1.18	0.3385
A*Y	1	39516.23	1.39	0.3031	48744.98	1.85	0.2454	25825.9	9.28	0.0382	219.05	0.67	0.4592	1659.03	0.73	0.4422
R*A*Y	1	9640.57	0.34	0.5911	465.66	0.02	0.9007	610.33	0.22	0.6639	203.04	0.62	0.4749	141.83	0.06	0.8155
Error[c]	4	28343.42			26347.62			2782.97			327.17			2285.23		
DC*Y	2	606.53	0.03	0.9711	8101.27	0.19	0.8345	339.37	0.12	0.8903	61.84	1.65	0.2512	249.39	1.32	0.3206
R*DC*Y	2	3884.18	0.19	0.8316	53185.06	1.22	0.3460	2092.75	0.73	0.5126	61.53	1.64	0.2527	280.39	1.48	0.2840
A*DC*Y	2	394.92	0.02	0.9810	29295.17	0.67	0.5385	466.39	0.16	0.8531	12.44	0.33	0.7270	438.47	2.31	0.1612
R*A*DC*Y	2	3306.25	0.16	0.8543	26278.58	0.60	0.5715	1198.63	0.42	0.6728	12.7	0.34	0.7223	287.86	1.52	0.2760
Error[d]	8	20588.12			43763.19			2877.65			37.48			189.55		

Appendix 5. Analysis of variance comparing the proportion saproxylic beetles of each trophic role reared from *Populus* coarse woody material, from Lac la Biche and Eureka River (Region); old and mature stands (Age); three decay classes of wood (Decay Class); snags and logs (Type); and 1993 and 1994 (Year).
(ᵃall three factor and higher interactions of region, age, decay class, and type pooled to form error;
ᵇall three factor interactions pooled to form error; † denotes significance at 95%).

Source	df	FUNGIVORE MS	F	P	PREDATOR MS	F	P	WOOD BORERS MS	F	P	SCAVENGERS MS	F	P	UNKNOWN MS	F	P
Region (R)	1	481.95	0.86	0.3779	58.13	0.31	0.5941	16.78	0.10	0.7545	2.41	0.18	0.6849	432.35	4.81	0.0560 †
Age (A)	1	179.74	0.32	0.5850	1679.05	8.82	0.0157 †	79.56	0.49	0.5004	0.03	0.00	0.9610	478.27	5.32	0.0466 †
R*A	1	304.19	0.54	0.4800	14.83	0.08	0.7865	502.1	3.11	0.1116	0.46	0.03	0.8574	435.91	4.85	0.0552 †
Decay Class (DC	2	959.57	1.71	0.2343	358.31	1.88	0.2077	971.2	6.02	0.0219 †	30.95	2.26	0.1605	74.22	0.83	0.4688
R*DC	2	32.82	0.06	0.9435	259.97	1.36	0.3036	80.71	0.50	0.6224	13.02	0.95	0.4226	54.19	0.60	0.5682
A*DC	2	293.19	0.52	0.6096	642.39	3.37	0.0807	40.12	0.25	0.7851	15.54	1.13	0.3640	69.48	0.77	0.4903
Type (T)	1	573.45	1.02	0.3381	395.12	2.07	0.1837	3894.86	24.13	0.0008 †	14.62	1.07	0.3287	0.1	0.00	0.9733
R*T	1	7.76	0.01	0.9089	75.65	0.40	0.5442	291.42	1.81	0.2120	45.46	3.31	0.1020	54.44	0.61	0.4566
A*T	1	179.52	0.32	0.5852	56.24	0.30	0.6000	64.45	0.40	0.5432	9.67	0.71	0.4227	2.39	0.03	0.8740
DC*T	1	18.71	0.03	0.9673	73.50	0.39	0.6906	335.6	2.08	0.1810	15.85	1.16	0.3574	197.62	2.20	0.1671
Error^a	9	560.37			190.47			161.41			13.71			89.95		
Year (Y)	1	191.16	0.38	0.5469	1292.66	7.48	0.0136 †	193.93	0.37	0.5516	200.4	16.14	0.0008 †	4094.01	35.82	0.0001 †
Y*R	1	3.79	0.01	0.9320	3.68	0.02	0.8855	5.64	0.01	0.9187	4.86	0.39	0.5389	188.21	1.65	0.2157
Y*A	1	66.44	0.13	0.7215	62.05	0.36	0.5565	1.94	0.00	0.9522	4.53	0.37	0.5533	125.07	1.09	0.3094
Y*DC	2	235.47	0.46	0.6358	76.99	0.45	0.6474	273.79	0.52	0.6033	35.49	2.86	0.0835	68.71	0.60	0.5588
Y*T	1	263.46	0.52	0.4802	0.09	0.00	0.9818	536.24	1.02	0.3264	13.94	1.12	0.3032	12.04	0.11	0.7492
Error^b	18	506.96			172.85			526.75			12.41			114.29		

Appendix 6. Analysis of variance comparing the proportion of saproxylic beetles of each trophic role collected with window-traps from *Populus* snags, from Lac la Biche and Eureka River (Region); old and mature stands (Age); three decay classes of wood (Decay Class); snags and logs (Type); and 1994 and 1995 (Year).
([a]stands within region by age interaction; [b]decay class by stands within region by age interaction; [c]year by stand within region by age; [d]decay class by year by stand within region by age interaction; † denotes significane at 95%).

		FUNGIVORES			PREDATORS			WOOD BORERS			SCAVENGERS			UNKNOWN		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	2639.16	4.07	0.1139	1.13	0.00	0.9619	102.67	0.66	0.4621	77.94	7.01	0.0571 †	982.59	89.02	0.0007 †
Age (A)	1	8569.92	13.21	0.0221 †	6172.25	14.06	0.0200 †	514.17	3.31	0.1432	0.32	0.03	0.8720	85.33	7.73	0.0498 †
R*A	1	2943.66	4.54	0.1002	1663.73	3.79	0.1234	31.21	0.20	0.6774	2.33	0.21	0.6708	88.48	8.02	0.0473 †
Error[a]	4	648.63			439.03			155.55			11.11			11.03		
Decay Class (DC	2	1099.65	3.04	0.1041	1933.3	5.09	0.0375 †	65.49	3.38	0.0865	58.6	3.12	0.0995	27.74	1.54	0.2722
R*DC	2	41.03	0.11	0.8941	120.32	0.32	0.7371	55.45	2.86	0.1157	22.26	1.19	0.3539	96.81	5.37	0.0333 †
A*DC	2	105.79	0.29	0.7539	52.72	0.14	0.8724	145.99	7.52	0.0145 †	7.12	0.38	0.6959	65.68	3.64	0.0751
R*A*DC	2	22.09	0.06	0.9411	356.69	0.94	0.4282	160.1	8.25	0.0114 †	3.47	0.18	0.8346	99.73	5.53	0.0311 †
Error[b]	8	361.43			379.66			19.4			18.76			18.04		
Year (Y)	1	470.69	0.63	0.4726	1996.52	23.32	0.0085 †	596.76	13.00	0.0226 †	28.93	3.36	0.1409	15.5	0.14	0.7278
R*Y	1	1446.93	1.93	0.2372	464.45	5.42	0.0803	5.21	0.11	0.7531	1.83	0.21	0.6692	165.06	1.48	0.2900
A*Y	1	333.39	0.44	0.5415	28.79	0.34	0.5931	585.82	12.76	0.0233 †	48.44	5.62	0.0768	40.72	0.37	0.5777
R*A*Y	1	787.67	1.05	0.3635	658.05	7.68	0.0502 †	129.33	2.82	0.1686	42.17	4.89	0.0915	6.07	0.05	0.8266
Error[c]	4	750.27			85.62			45.91			8.62			111.16		
DC*Y	2	193.43	0.69	0.5297	78.33	0.97	0.4195	18.56	0.16	0.8538	2.82	0.26	0.7775	9.95	0.35	0.7170
R*DC*Y	2	224.67	0.80	0.4823	116.51	1.44	0.2917	14.55	0.13	0.8830	9.64	0.89	0.4490	2.96	0.10	0.9029
A*DC*Y	2	120.48	0.43	0.6653	199.61	2.47	0.1459	64.33	0.56	0.5928	10.3	0.95	0.4275	15.64	0.55	0.5998
R*A*DC*Y	2	71.78	0.26	0.7806	154.12	1.91	0.2100	16.31	0.14	0.8700	13.91	1.28	0.3297	16.26	0.57	0.5884
Error[d]	8	280.85			80.74			115.14			10.87			28.69		

Appendix 7. Analysis of variance comparing the number of species, genera, families, and standardized abundance from saproxylic beetles collected with window-traps on *Populus* snags from old and mature stands (Age); forest and harvested stands (Stand Type); and three decay classes of wood (Decay Class); near Lac la Biche Alberta, 1995.
([a]stands within age by cut interaction; [b]decay class by stands within age by cut interaction; † denotes significance at 95%).

		Species			Genera			Families			Abundance		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Age (A)	1	560.14	4.39	0.1043	449.07	4.57	0.0994	213.36	5.33	0.0821	511925	1.04	0.3659
Stand Type (T)	1	4231.91	33.15	0.0045 †	3312.72	33.71	0.0044 †	1152.72	28.81	0.0058 †	11280738	22.88	0.0088 †
A*T	1	25.78	0.20	0.6764	15.56	0.16	0.7109	5.45	0.14	0.7307	4046	0.01	0.9322
Error[a]	4	127.65			98.27			40.00			493140		
Decay Class (DC)	2	68.34	0.97	0.4239	50.18	0.74	0.5094	0.11	0.01	0.9940	1859402.7	7.93	0.0159 †
A*DC	2	89.34	1.27	0.3380	94.96	1.41	0.3063	7.26	0.37	0.7009	845592.2	3.61	0.0839
T*DC	2	36.97	0.53	0.6125	30.47	0.45	0.6538	29.32	1.51	0.2850	184321.9	0.79	0.4921
A*T*DC	2	146.55	2.09	0.1947	134.67	2.00	0.2060	25.63	1.32	0.3263	156524.6	0.67	0.5429
Error[b]	7	70.26			67.46			19.42			234524		

Appendix 8. Analysis of variance comparing absolute abundance of saproxylic beetles in each trophic role collected from *Populus* coarse woody material, from old and mature stands (Age); forest and harvested stands (Stand Type); and from three decay classes of wood (Decay Class); near Lac la Biche Alberta, 1995.

(ᵃstands within the age by cut interaction; ᵇdecay class by stands within age by cut interaction; † denotes significance at 95%).

		FUNGIVORE			PREDATORS			WOOD BORERS			SCAVENGERS			UNKNOWN		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Age (A)	1	445112.70	7.43	0.0527 †	1075567	4.08	0.1137	105507.05	12.32	0.0247 †	46.18	0.05	0.8344	758.41	0.78	0.4276
Stand Type (T)	1	2786340.00	46.49	0.0024 †	695235.2	2.63	0.1799	225124.09	26.28	0.0069 †	27561.45	29.71	0.0055 †	46290.04	47.47	0.0023 †
A*T	1	161521.70	2.69	0.1760	98978.3	0.38	0.5734	26651.54	3.11	0.1525	26.50	0.03	0.874	51.95	0.05	0.8288
Error^a	4	239750.50			263931.9			8565.57			927.72			975.07		
Decay Class (DC)	2	355574.24	5.95	0.0309 †	329809.48	3.91	0.0724	33042.89	2.02	0.2024	1595.75	2.32	0.1689	1407.75	1.12	0.3782
A*DC	2	79285.14	1.33	0.3246	308067.33	3.65	0.0819	7818.00	0.48	0.6383	267.83	0.39	0.6916	3822.52	3.04	0.1119
T*DC	2	203802.27	3.41	0.0924	3526.84	0.04	0.9593	3530.55	0.22	0.6107	726.43	1.05	0.3977	1636.11	1.30	0.3305
A*T*DC	2	44735.70	0.75	0.5074	2483.1	0.03	0.9711	12524.62	0.77	0.4997	514.81	0.75	0.5079	3791.17	3.02	0.1135
Error^b	7	59745.60			84315.1			16323.37			688.66			1256.14		

Appendix 9. Analysis of variance comparing proportion of saproxylic beetles of each trophic role collected from *Populus* coarse woody material, from old and mature stands (Age); forest and harvested stands (Stand Type); and from three decay classes of wood (Decay Class); near Lac la Biche Alberta, 1995.
(ᵃstands within the age by cut interaction; ᵇdecay class by stands within age by cut interaction; † denotes significance at 95%).

		FUNGIVORE			PREDATORS			WOOD BORERS			SCAVENGERS			UNKNOWN		
Source	**df**	**MS**	**F**	**P**	**MS**	**F**	**P**	**MS**	**F**	**P**	**MS**	**F**	**P**	**MS**	**F**	**P**
Age (A)	1	9054.80	36.81	0.0037 †	4342.2	11.05	0.0293 †	762.57	28.87	0.0058 †	3.66	0.65	0.4641	12.68	0.56	0.4949
Stand Type (T)	1	93.91	0.38	0.5701	7.93	0.02	0.8939	20.17	0.76	0.4314	78.14	13.93	0.0202 †	0.67	0.03	0.8706
A*T	1	3.38	0.01	0.9122	32.22	0.08	0.7888	0.07	0.00	0.9607	0.96	0.17	0.6994	6.67	0.30	0.6154
Error^a	4	246.01			392.87			26.41			5.61			22.54		
Decay Class (DC)	2	290.31	1.22	0.3502	291.99	3.28	0.0988	39.21	0.53	0.6124	25.44	9.85	0.0092 †	0.55	0.02	0.9787
A*DC	2	70.58	0.30	0.7517	334.42	3.76	0.0779	132.68	1.78	0.2370	5.24	2.03	0.2016	24.41	0.96	0.4296
T*DC	2	905.97	3.82	0.0757	364.12	4.09	0.0665	18.02	0.24	0.7914	3.04	1.18	0.3617	34.97	1.37	0.3150
A*T*DC	2	165.02	0.70	0.5303	163.38	1.84	0.2285	32.11	0.43	0.6659	2.57	1.00	0.4158	21.86	0.86	0.4651
Error^b	7	237.29			88.98			74.49			2.58			25.55		

Appendix 10. An analysis of variance testing the mean number of species, genera, families and standardized abundance of beetles collected from newly created *Populus* coarse woody material, in two ages of boreal forest near Lac la Biche and Eureka River, Alberta in 1994 and 1995. Treatment effects refer to a comparison of screened and unscreened wood sections. Section effects compare data from snags, stumps and logs. The number of taxa and abundance was standardized to 150 rearing days and 0.1m3 of wood.

(^{a}stands within region by age interaction; ^{b}section by treatment by stand within the region by age interaction; ^{c}year by stand within the region by age interaction; and ^{d}total error;† denotes significance at 95% confidence.)

		Species			Genera			Families			Abundance		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	0.05	0.01	0.9393	0.03	0.00	0.9463	0.16	0.04	0.8422	824.73	0.28	0.6168
Age (A)	1	79.09	9.97	0.0196 †	58.82	8.34	0.0278 †	39.89	10.27	0.0185 †	4930.36	1.66	0.2447
R*A	1	7.20	0.91	0.3775	5.51	0.78	0.4107	5.51	1.42	0.2786	7328.17	2.47	0.1670
Error^a	6	7.93			7.05			3.88			2964.91		
Treatment (T)	1	106.20	35.63	0.0001 †	102.34	38.74	0.0001 †	74.35	43.01	0.0001 †	51290.31	17.28	0.0002 †
T*R	1	1.80	0.60	0.4428	0.86	0.33	0.5705	0.61	0.35	0.5559	1812.37	0.61	0.4403
T*A	1	3.71	1.25	0.2723	2.77	1.05	0.3131	0.22	0.13	0.7224	8795.95	2.96	0.0948
T*R*A	1	14.45	4.85	0.0350 †	14.73	5.58	0.0244 †	13.61	7.87	0.0085 †	4506.49	1.52	0.2268
Section (S)	2	3.82	1.28	0.2913	3.13	1.19	0.3178	1.46	0.84	0.4391	6637.21	2.24	0.1233
S*R	2	0.67	0.23	0.7975	0.27	0.10	0.9010	0.63	0.37	0.6956	495.58	0.17	0.8469
S*A	2	3.47	1.16	0.3248	4.46	1.69	0.2005	2.85	1.65	0.2077	974.50	0.33	0.7225
S*R*A	2	2.52	0.85	0.4375	3.00	1.14	0.3333	1.77	1.03	0.3688	36.79	0.01	0.9877
S*T	2	2.73	0.92	0.4097	2.84	1.08	0.3522	1.68	0.97	0.3893	5205.44	1.75	0.1893
S*T*R	2	3.15	1.06	0.3589	2.01	0.76	0.4741	2.11	1.22	0.3080	425.07	0.14	0.8671
S*T*A	2	4.90	1.65	0.2086	5.61	2.12	0.1362	3.03	1.75	0.1892	2145.18	0.72	0.4931
Error^b	32	2.98			2.64			1.72			2967.57		
Year (Y)	1	5.70	1.71	0.2391	3.37	1.39	0.2837	8.77	8.42	0.0273 †	32991.21	15.26	0.0079 †
Y*R	1	0.08	0.03	0.8757	0.06	0.03	0.8727	0.23	0.17	0.6944	2760.08	1.28	0.3017
Y*A	1	11.57	3.47	0.1119	15.05	6.19	0.0473 †	5.84	6.31	0.0457 †	11837.50	5.48	0.0578 †
Y*R*A	1	0.05	0.01	0.9066	0.01	0.00	0.9817	0.23	0.17	0.6944	2246.37	1.04	0.3474
Error^c	6	3.33			2.43			1.32			2161.94		
Y*T	1	2.45	1.11	0.2981	2.11	0.99	0.3258	0.61	0.38	0.5421	21767.28	9.77	0.0033 †
Y*T*R	1	2.45	1.11	0.2981	2.11	0.99	0.3258	1.51	0.93	0.3397	3488.50	1.57	0.2183
Y*T*A	1	12.03	5.46	0.0247 †	14.00	6.57	0.0144 †	5.63	3.48	0.0697	16497.03	7.40	0.0097 †
Y*S	2	9.73	4.42	0.0186 †	10.63	4.98	0.0118 †	6.64	4.10	0.0241 †	13116.22	5.89	0.0058 †
Y*S*R	2	5.08	2.31	0.1129	3.16	1.49	0.2390	1.51	0.93	0.4021	565.36	0.25	0.7772
Y*S*A	2	2.55	1.16	0.3237	2.51	1.18	0.3193	1.43	0.89	0.4207	1263.87	0.57	0.5717
Y*S*T	2	2.25	1.02	0.3683	0.75	0.36	0.7031	0.70	0.43	0.6520	9996.34	4.49	0.0176 †
Error^d	39	2.20			2.13			1.61			2228.12		

Appendix 11. An analysis of variance testing the proportion of each trophic role of beetles collected from newly created *Populus* coarse woody material, in two ages of boreal forest near Lac la Biche and Eureka River, Alberta in 1994 and 1995. Treatment effects refer to a comparison of screened and unscreened wood sections. Section effects compare data from snags, stumps and logs. The number of taxa and abundance was standardized to 150 rearing days and 0.1m3 of wood.

([a]stands within region by age interaction; [b]section by treatment by stand within the region by age interaction; [c]year by stand within the region by age interaction; and [d]total error;† denotes significance at 95% confidence.)

		FUNGIVORE			PREDATOR			WOOD BORERS			SCAVENGERS			UNKNOWN		
Source	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Region (R)	1	2287.05	1.68	0.2421	2070.88	2.37	0.1749	1147.81	1.60	0.2528	70.02	0.93	0.3716	200.80	0.57	0.4798
Age (A)	1	1554.18	1.14	0.3259	5597.68	6.39	0.0448 †	410.30	0.57	0.4781	145.28	1.93	0.2137	29.20	0.08	0.7836
R*A	1	520.04	0.38	0.5588	3296.11	3.77	0.1004	67.47	0.09	0.7695	89.03	1.19	0.3181	36.17	0.10	0.7600
Error[a]	6	1358.24			875.23			717.46			75.12			353.94		
Treatment (T)	1	828.79	0.73	0.4007	26.78	0.03	0.8731	3789.46	9.79	0.0037	115.46	1.42	0.2426	183.77	0.50	0.4839
T*R	1	0.38	0.00	0.9856	2531.72	2.45	0.1274	536.33	1.39	0.2479	146.28	1.80	0.1897	157.20	0.43	0.5171
T*A	1	5006.84	4.38	0.0443 †	176.84	0.17	0.6819	137.58	0.36	0.5553	70.19	0.86	0.3602	398.27	1.09	0.3049
T*R*A	1	2303.65	2.02	0.1653	1644.91	1.59	0.2163	60.13	0.16	0.6961	173.25	2.13	0.1545	412.11	1.12	0.2968
Section (S)	2	2890.85	2.53	0.0955	10151.18	9.82	0.0005 †	2095.55	5.41	0.0094 †	166.60	2.05	0.1459	297.90	0.81	0.4524
S*R	2	1395.52	1.22	0.3082	1706.78	1.65	0.2078	167.87	0.43	0.6519	99.76	1.22	0.3073	421.66	1.15	0.3291
S*A	2	1884.29	1.65	0.2082	4192.23	4.06	0.0268 †	111.52	0.29	0.7516	169.17	2.08	0.1419	244.27	0.67	0.5203
S*R*A	2	2145.86	1.88	0.1694	647.03	0.63	0.5412	104.02	0.27	0.7661	74.59	0.92	0.4105	222.57	0.61	0.5508
S*T	2	311.54	0.27	0.7631	314.12	0.30	0.7401	37.82	0.10	0.9072	78.11	0.96	0.3941	189.08	0.52	0.6017
S*T*R	2	131.32	0.11	0.8918	447.82	0.43	0.6522	1.67	0.00	0.9957	187.86	2.31	0.1160	887.40	2.42	0.1048
S*T*A	2	6608.33	5.78	0.0072 †	1130.50	1.09	0.3472	488.10	1.26	0.2972	51.73	0.63	0.5365	154.19	0.42	0.6600
Error[b]	32	1142.65			1033.75			387.17			81.46			366.32		
Year (Y)	1	627.23	0.16	0.7065	3830.50	2.08	0.1992	7129.18	18.00	0.0054 †	142.92	1.84	0.2238	1797.71	3.11	0.1283
Y*R	1	1490.12	0.37	0.5650	2670.72	1.45	0.2737	3567.43	9.01	0.0240 †	116.71	1.50	0.2663	6.81	0.01	0.9171
Y*A	1	71.81	0.02	0.8981	329.01	0.18	0.6872	44.00	0.11	0.7502	163.37	2.10	0.1972	76.87	0.13	0.7279
Y*R*A	1	977.13	0.24	0.6395	1577.36	0.86	0.3903	198.91	0.50	0.5051	75.01	0.97	0.3638	853.50	1.48	0.2700
Error[c]	6	4020.55			1840.57			1592.39			77.71			578.04		
Y*T	1	1.12	0.00	0.9731	1194.14	1.31	0.2601	310.69	0.79	0.3782	70.02	0.81	0.3743	87.06	0.25	0.6168
Y*T*R	1	2053.75	2.11	0.1544	2713.85	2.97	0.0928	2401.74	6.14	0.0176 †	211.12	2.44	0.1267	1640.21	4.79	0.0346 †
Y*T*A	1	424.72	0.44	0.5129	97.87	0.11	0.7453	0.05	0.00	0.9902	50.43	0.58	0.4502	68.61	0.20	0.6568
Y*S	2	233.87	0.24	0.7877	677.95	0.74	0.4830	31.29	0.08	0.9232	187.86	2.17	0.1281	1390.26	4.06	0.0250 †
Y*S*R	2	2135.36	2.19	0.1252	1597.92	1.75	0.1875	945.36	2.42	0.1024	85.55	0.99	0.3819	194.43	0.57	0.5712
Y*S*A	2	729.25	0.75	0.4796	819.88	0.90	0.4161	576.38	1.47	0.2415	114.22	1.32	0.2795	279.68	0.82	0.4490
Y*S*T	2	884.63	0.91	0.4115	182.51	0.20	0.8199	955.82	2.44	0.1000	57.51	0.66	0.5209	152.04	0.44	0.6445
Error[d]	39	973.87			914.21			391.07								

Appendix 12. Analysis of variance testing mean wood hardness measurements from *Populus* log, stump and snag wood sections, from two ages of boreal mixedwood forest stands near Lac al Biche and Eureka River, Alberta, 1994 and 1995. Three measurements were made on each wood section, and the mean value from each section tested. See text for explanation of wood measurement.

([a]stand within region by age interaction; [b]section by trees within the treatment by stand within region by age interaction; [c]year by stand within the region by age interaction; [d]total error; †denotes significance at 95%.)

Source	df	MS	F	P
Region (R)	1	2636.30	49.52	0.0004 †
Age (A)	1	275.80	5.18	0.0631
R*A	1	183.80	3.45	0.1125
Error[a]	6	53.23		
Treatment (T)	1	35.70	1.74	0.1926
T*R	1	26.10	1.27	0.2650
T*A	1	5.70	0.28	0.6000
T*R*A	1	24.90	1.21	0.2749
Section (S)	2	6.60	0.32	0.7262
S*R	2	42.60	2.10	0.1353
S*A	2	2.70	0.13	0.8782
S*R*A	2	36.50	1.77	0.1788
S*T	2	2.80	0.14	0.8714
S*T*R	2	34.90	1.70	0.1922
S*T*A	2	2.60	0.12	0.8834
Error[b]	60	20.58		
Year (Y)	1	0.17	0.01	0.9389
Y*R	1	18.42	0.66	0.4485
Y*A	1	38.23	1.36	0.2871
Y*R*A	1	4.68	0.17	0.6970
Error[c]	6	28.03		
Y*S	2	6.39	0.27	0.7672
Y*S*R	2	11.89	0.49	0.6121
Y*S*A	2	4.49	0.19	0.8300
Y*T*S	2	11.20	0.47	0.6288
Error[d]	60	24.04		